

Mark-Recapture Experiment for the 2009 Chinook Salmon Spawning Escapement in the Atnarko River

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MARK-RECAPTURE EXPERIMENT FOR THE 2009 CHINOOK SALMON
SPAWNING ESCAPEMENT IN THE ATNARKO RIVER

by

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ABSTRACT

Vélez-Espino, L.A., Mullins, G., Willis, J., Krimmer, A. and Levesque, W. Mark-recapture experiment for the 2009 Chinook salmon spawning escapement in the Atnarko River. Can. Manuscr. Rep. Fish. Aquat. Sci. 2930: xii + 51 p.

Two-sample, closed population estimates of spawning escapement in Pacific salmon populations have constituted a common practice. This pooled-Petersen mark-recapture approach seems appropriate for cases where closed-population assumptions are met, but could ignore major bias sources if violations to these assumptions are overlooked. In addition, the richness of information commonly generated by many Pacific salmon mark-recapture studies is not being utilized when following a pooled-Petersen protocol, therefore missing important opportunities to enrich our knowledge of salmon ecology. The main goals of this paper are: (i) to provide an estimate of the 2009 Chinook salmon (*Oncorhynchus tshawytscha*) spawning escapement in the Atnarko River applying the standard pooled-Petersen mark-recapture experiment; (ii) to apply an alternative and robust approach to spawning escapement estimation within a model selection framework encompassing suites of open-population and closed-population maximum likelihood estimators based on individual encounter histories and formal testing of primary closed-population assumptions; and, (iii) to demonstrate the use of information provided by individual encounter histories from mark-recapture experiments allowing the reconstruction of migration phenologies and the estimation of stream residence times.

Spawning escapements of 3,593 (95% CI: 3,077 – 4,108) females, 5,636 (95% CI: 4,640 – 6,632) males, and 1,532 (95% CI: 1,028 – 2,035) jacks were estimated with the Petersen model for a total spawning escapement of 10,761 (95% CI: 8,745 – 12,775; CV = 5.7%) fish. These numbers exclude the fish removed from the system for hatchery purposes (969).

Using the maximum likelihood model selection approach, closure assumptions were violated and best open-population escapement estimates for females, males, and jacks were 8,232 (SE: 615.2), 7,877 (SE: 513.2), and 4,159 (SE: 796.5), respectively, for a total escapement estimate of 20,268 (95% CI: 16,985 – 24,601; CV = 9.5%). These numbers represent the fish escaping the terminal fisheries and entering the study area and include the fish removed from the system for hatchery purposes (969) and their removal's effect on capture probabilities. Accounting for the survival rates of Chinook salmon within the study period (0.95 for females, 0.94 for males, and 0.95 for jacks) left an average of 19,157 total effective natural spawners.

The analysis of scales from a sample of salmon carcasses indicated that about 80% of the spawners consisted of age-3 and age-4 individuals with 100% of the age-3 fish and 91.4% of the age-4 fish exhibiting ocean-type life history. Only 37.9% of the age-5 fish and 28.6% of the age-6 fish exhibited this life history type. The analysis of coded-wire-tag data from a sample of adipose-fin-clipped carcasses indicated that 37.0%

of the females, 50.6% of the males, and 61.4% of the jacks in the spawning escapement were of hatchery origin, which translated into an overall hatchery contribution of 49%.

Important sources of uncertainty in the mark-recapture experiment of the 2009 Atnarko Chinook spawning escapement were associated to a high tag-loss rate, inconsistencies in the record of recaptures and losses-on-capture, and the return to the system of fish previously removed for hatchery purposes. Although these factors influence escapement estimates of mark-recapture experiments in general, they are particularly crucial in analyses dependent on individual encounter histories. The identification of these issues is expected to improve the reliability of spawning escapement estimates derived from robust analytical approaches in future years. It is herein argued that the intensive and extensive sampling effort currently at work in the Atnarko should be capitalized on by following an experimental approach characterized by the evaluation of closure assumptions, mark-recapture model selection, and the optimization of the use of information.

RÉSUMÉ

Vélez-Espino, L.A., Mullins, G., Willis, J., Krimmer, A. and Levesque, W. Mark-recapture experiment for the 2009 Chinook salmon spawning escapement in the Atnarko River. Can. Manuscr. Rep. Fish. Aquat. Sci. 2930: xii + 51 p.

L'estimation de l'échappée de géniteurs des populations de saumon du Pacifique, à partir de deux échantillonnages d'une population fermée, est une pratique courante. La méthode de Petersen par marquage-recapture semble appropriée, lorsque l'hypothèse d'une population fermée est corroborée, mais pourrait omettre d'importantes sources de biais si on ne prend pas en compte les manquements à cette hypothèse. De plus, l'énorme quantité d'information générée habituellement par de nombreuses études de marquage-recapture du saumon du Pacifique ne sont pas prises en compte quand on applique un protocole de Petersen groupé, de sorte qu'on rate d'importantes occasions d'enrichir la banque de connaissances sur l'écologie du saumon. Les principaux objectifs du présent document sont les suivants : (i) fournir une estimation de l'échappée de géniteurs du saumon quinnat (*Oncorhynchus tshawytscha*) dans la rivière Atnarko en 2009, en utilisant la méthode groupée de marquage-recapture normalisée de Petersen; (ii) appliquer une méthode différente et robuste pour estimer l'échappée de géniteurs à l'intérieur d'un cadre de sélection de modèle comprenant des ensembles d'estimateurs de probabilité maximale des populations ouvertes et fermées, en fonction de l'historique des observations ponctuelles et des vérifications formelles de l'hypothèse primaire d'une population fermée; et (iii) démontrer l'utilisation des données fournies par l'historique des observations ponctuelles tiré des expériences de marquage-recapture, permettant la reconstruction des phénologies de migration et l'estimation des temps de séjour dans un cours d'eau.

On a estimé une échappée de 3 593 géniteurs femelles (intervalle de confiance de 95 % : 3 077 – 4 108), de 5 636 géniteurs mâles (intervalle de confiance de 95 % : 4 640 – 6 632) et de 1 532 géniteurs mâles matures (intervalle de confiance de 95 % : 1 028 – 2 035) à l'aide du modèle de Petersen, ce qui donne une échappée totale de géniteurs de 10 761 individus (intervalle de confiance de 95 % : 8 745 – 12 775; CV = 5,7 %). Ces nombres ne comprennent pas les individus retirés du système aux fins d'élevage (969).

En appliquant l'approche de sélection d'un modèle de probabilité maximale, on constate que les hypothèses de fermeture n'ont pas été respectées, et les meilleures estimations de l'échappée, dans une population ouverte, pour les femelles, les mâles et les mâles matures ont été les suivantes : 8 232 (échappée de géniteurs [EG] : 615,2), 7 877 (EG : 513,2) et 4 159 (EG : 796,5), respectivement, ce qui donne une échappée totale estimée de 20 268 individus (intervalle de confiance de 95 % : 16 985 – 24 601; CV = 9,5 %). Ces nombres correspondent aux individus qui échappent aux pêches terminales et entrent dans la zone d'étude, comprennent les individus retirés du système aux fins d'élevage (969) et tiennent compte de l'effet qu'a leur retrait sur les probabilités de capture. En tenant compte des taux de survie du saumon quinnat au cours de la période d'étude (0,95 pour les femelles, 0,94 pour les mâles et 0,95 pour les mâles matures), on obtient une moyenne de 19 157 reproducteurs naturels efficaces.

L'analyse des écailles d'un échantillon de carcasses de saumons a permis de déterminer qu'environ 80 % des reproducteurs étaient des individus de trois et de quatre ans, et que 100 % des individus de trois ans et 91,4 % des individus de quatre ans présentaient un cycle vital de type océanique. Seulement 37,9 % des individus de cinq ans et 28,6 % des individus de six ans présentaient ce type de cycle vital. L'analyse des données de micromarques magnétisées codées d'un échantillon de carcasses de saumons dont la nageoire adipeuse avait été coupée a permis de constater que 37,0 % des femelles, 50,6 % des mâles et 61,4 % des mâles matures, compris dans l'échappée de géniteurs, provenaient de l'élevage, ce qui signifie que la contribution globale de l'élevage est de 49 %.

L'expérience de marquage-recapture lors de l'échappée de géniteurs du saumon quinnat dans la rivière Atnarko, en 2009, comportait d'importantes sources d'incertitude associées au taux élevé de perte des micromarques, aux irrégularités dans la consignation des recaptures et des pertes au moment de la capture et au retour, dans le système, des individus retirés aux fins d'élevage. Ces facteurs ont une incidence sur les estimations de l'échappée lors des expériences de marquage-recapture de façon générale, mais ils s'avèrent particulièrement essentiels dans les analyses qui dépendent de l'historique des observations ponctuelles. L'identification de ces facteurs devrait améliorer la fiabilité des estimations de l'échappée de géniteurs calculées au moyen de méthodes d'analyse robustes dans les années à venir. Nous proposons, dans le présent document, de tirer parti des travaux d'échantillonnage intensifs et approfondis en cours à la rivière Atnarko en suivant une méthode expérimentale caractérisée par l'évaluation de l'hypothèse de fermeture, la sélection d'un modèle de marquage-recapture et l'optimisation de l'utilisation des données.

1. INTRODUCTION

1.1 The Atnarko River in perspective

A recent report of the coded wire tag (CWT) workgroup of the Pacific Salmon Commission (PSC) identified a lack of sufficient CWT indicator stock coverage of production regions or stock aggregates in British Columbia (Pacific Salmon Commission Coded Wire Tag Workgroup 2008). It was recognized that major Chinook salmon (*Oncorhynchus tshawytscha*) production areas and life histories are poorly represented by CWT indicator stocks currently used for assessments by the PSC technical committees. Currently, there is no appropriate indicator of the biological and fishery characteristics of Chinook salmon stocks entering the central coast area of British Columbia. In 2008, the CWT workgroup of the PSC recommended agencies to evaluate their escapement estimation and sampling programs where CWT tagged Chinook are present on the spawning grounds (Pacific Salmon Commission Coded Wire Tag Workgroup 2008). A review of the sampling programs indicated that spawning ground sampling is often not in place or inadequate and therefore generating highly uncertain escapement estimates. It is believed that an indicator program in the central coast can be functional almost immediately if funding is available for an escapement program in the Atnarko River (Pacific Salmon Commission Coded Wire Tag Workgroup 2008). Although Atnarko Chinook have been CWTed for many years in the Snootli Hatchery, Bella Coola BC, some issues have been identified as limiting the quality of information: bias in estimates of total escapement, data coordination reporting problems, and limitations of funds to conduct robust and effective sampling and analysis (Pacific Salmon Commission Coded Wire Tag Workgroup 2008). These problems have also precluded the inclusion of Atnarko Chinook in exploitation rate analyses conducted by the PSC Chinook Technical Committee (CTC). As a result, Fisheries and Oceans Canada initiated in 2009 a five-year mark-recapture program in the Atnarko River with the purpose of improving escapement estimates for early summer Chinook. This program represents a unique opportunity to implement modern mark-recapture experiments with the potential to generate robust estimates that not only comply with CTC data standards but also test relevant assumptions associated with specific models, thoroughly use the information generated by the experiment, and comply with the recommendations of the CWT expert panel.

Chinook salmon CWT indicators nearest to the Atnarko are the Kitsumkalum in north BC and Chilliwack in south BC in mainland and Quinsam in the east coast of Vancouver Island. While the northern BC CTC model stock group is represented by the Kitsumkalum, the Central BC group (currently represented by Wannock, Chuckwalla, and Dean Rivers), does not have an exploitation rate indicator. Differences in life history, ecology, and molecular genetics between Kitsumkalum Chinook and Atnarko Chinook determine their corresponding stocks being part of separate conservation units in Canada (Holtby and Ciruna 2007). In terms of life history, Atnarko Chinook exhibits a life history type that is predominantly ocean-type (Pestal 2004) while the Kitsumkalum Chinook is mostly stream type (McNicol 1999). Historical recoveries of CWTs show an Atnarko Chinook distribution across numerous Pacific Salmon Commission (PSC) fisheries with the majority of recoveries occurring in the Alaska troll fishery (Appendix

A). Atnarko Chinook are also intercepted to a lesser extent in northern and central BC marine sport fisheries (~1%). In contrast, most of the Kitsumkalum Chinook recoveries proceed in similar proportions from Alaska troll and northern net and troll BC fisheries (McNicol 1999).

Although estimates of Bella Coola watershed Chinook escapement are available from 1950 (BCWCS 2007; see also Appendix B) and escapement estimates for the Atnarko proper exist from 1980 (Pestal 2004, Riddell 2004; see also Appendix C), mark-recapture experiments have been conducted only sporadically: 1984-1986 (Slaney 1986, Web and Sutherland 1986) and 2001-2003 (Sturhahn 2009). Enumeration methods commonly employed have included carcass surveys, drift net surveys, adults collected in seine nets to provide brood stock for the Snootli Creek hatchery, commercial catch information collected from aerial gear counts, sales slips, dockside monitoring, observer records from drifts and catches in the Nuxalk FSC fishery, and catch and effort data from the recreational fishery (Pestal 2004). By the beginning of the 1990s, suitability maps combined with expansion factors, fishery officer enumeration areas based on drift counts in high-density river sections, area under the curve estimation (see English et al. 1992 for a description of this method), and carcass recoveries (Pitre 1991) constituted common methods to enumerate adult Chinook in the Atnarko. For most of the last decade, fishery managers have used the average of three population estimates to determine the final escapement estimate for Atnarko Chinook. These methods generate independent population estimates based on (i) CPUE during brood stock collection, (ii) carcasses handled during deadpitch, and (iii) drift surveys (Petersen estimates were included in the average for years 2001-2003; Appendix B). And although the simplicity and low cost of those three methods has allowed the continuous monitoring of Atnarko escapement, they require to be contrasted and, if possible, calibrated with higher-quality data such as provided by well-planned mark-recapture experiments.

Atnarko Chinook are easily captured and recovered as this system is not as susceptible to fall flooding as many other coastal Chinook systems (BCWCS 2007). The close proximity of qualified hatchery staff and personnel also reduce risk inherent with conducting mark-recapture programs on remote systems. Given past mark-recapture and deadpitch programs conducted on the Atnarko there exists a good understanding of effort requirements for sufficient tag application as well as carcass recovery. Past mark-recapture programs have been successful in terms of recovery rates, thus providing estimates with low coefficients of variation (Appendix D). Tagging and recovery efforts during the 2009 mark-recapture experiment, and the alternative application of modern capture-recapture analyses, are expected to yield results that meet or exceed the CTC bilateral data standards while laying the basis for future studies.

Good-quality Atnarko Chinook spawning escapement is important not only for the reasons mentioned above but also to improve planning of terminal fisheries (pre-season and in-season), improved accuracy of CTC abundance indices for mixed stocks in north British Columbia and southeast Alaska and fishery planning, improved information to support First Nations Treaty negotiation, and to better meet Canada's fiduciary responsibilities. Moreover, robust spawning escapement estimation is expected to enrich

our knowledge of the population dynamics of coastal Chinook stocks in the North-Central BC stock group, with the potential to assist the development of a salmon monitoring program to learn how stocks in the coastal transition zone of mixed ocean and stream type life history respond to climate changes. Lastly, in conjunction with improvements in sampling design, robust escapement estimation is expected to support the Wild Salmon Policy action step 1.3 of Strategy 1, which emphasizes the monitoring and status assessment of indicator systems and the optimization of monitoring costs (DFO 2005).

1.2 Hatchery contribution

Atnarko hatchery Chinook production has averaged around 2 million annually with 150 000 of released fry having been marked with CWT's. This enhancement has continued since the mid 1980's, usually splitting the release of juvenile fish between upper and lower Atnarko in an attempt to cover potential differences in outmigration timing between the areas. In addition, release timings are structured with yearling and smolt releases to match the various life history strategies present. Direct hatchery contributions are measured and compared using several methods. The annual Chinook deadpitch program is believed to be the least biased of the methods and historical mark presence data suggests an average hatchery contribution of approximately 40% of the spawning runs (Personal communication; Julian Sturhahn, Fisheries and Oceans Canada Campbell River, BC). In some years, an estimated 30-40% of the total Chinook escapement to the Bella Coola watershed is of hatchery origin (Hilland and Lehman 2005).

1.3 Study Area

The Atnarko River feeds the Bella Coola River and is situated in Statistical Area 8 on the Central Coast of B.C. (Figure 1). This system is located north of Cape Caution and resides within the Northern Fund region of the PST. The Atnarko River drains a 2,440 km² watershed, merging with the Talchako River to form the Bella Coola River (see Figure 2). With the exception of Charlotte Lake and the headwaters of the Hotnarko River, the Atnarko and its tributaries are situated within the boundaries of Tweedsmuir Provincial Park. The Atnarko can be divided into three river segments with specific biotic and abiotic attributes. The upper segment has many sections with deep and large holding areas that constitute high quality spawning areas. Overall the spawning habitat is excellent with the exception of the lower part of the upper section where the river gradient decreases, resulting in very slow water velocities and virtually no spawning habitat. The middle segment is characterized by sections with larger substrate, boulders, and increased gradient drops. Higher water velocities result in a generally lower quality spawning habitat. Holding in this section is limited and spawning is generally spread out. The lower segment is characterized by braided sections and dominated by high quality spawning habitat in its middle and lower sections. The upper part of this section does have some areas with large boulders and large substrate (due to increases in the river

gradient), and thus limited areas to spawn. Most of the holding areas are small to moderate in size, with the exception of Alger's pool (the largest holding area on the river). These holding areas have suitable spawning habitat located both above and below.

The Atnarko Chinook population is summer timed with a predominantly ocean-type life history strategy. This population is the primary contributor to the Bella Coola-Dean Conservation Unit (Holtby and Ciruna 2007). Distribution of Chinook salmon is mainly concentrated in the Atnarko River; although, some Chinook utilize the waters of the Talchako and tributaries in the Lower Bella Coola (BCWCS 2007). Within the Atnarko River, Chinook are primarily distributed from Hotnarko River to Janet Creek in the upper Atnarko River, and from Alger Creek to the confluence of the Talchako River in the lower Atnarko River (DFO 1989; FISS 2005; Figure 2). Since the majority of Chinook entering the Bella Coola spawn in the Atnarko, estimating the Chinook spawning escapement in the Atnarko is of primary importance. There is also a small group of lower Bella Coola tributary spawners which are enumerated annually using stream walks. These Bella Coola spawners are believed to make up a very small component of the overall system with historical counts of approximately 300 fish annually (Personal communication; Julian Sturhahn, Fisheries and Oceans Canada Campbell River, BC). Bella Coola watershed escapement has been estimated using a change-in-ratio method based on differences in observed mark rates between the Atnarko deadpitch and the lower Bella Coola First Nations net fishery (see Figure 3).

1.4 Mark-recapture experiments (background information)

Two-sample, closed population estimates of spawning escapement in salmon populations have constituted a common practice in Pacific salmon studies. Petersen (or variants of the Petersen) estimates have been applied regularly even in the presence of rich encounter information provided by mark-recapture experiments. Normally, the experiments are divided into two main phases: tagging of live fish and recovery of carcasses at the end of the spawning period. During the first phase several sampling occasions take place in which fish are tagged with primary (e.g., metal tags stapled in the operculum) and secondary (e.g., punch holes in the operculum) marks and released alive. Ideally, in each of these sampling occasions records are kept of the number of fish tagged and released alive, fish removed for hatchery purposes, fish incidentally killed as a result of the experiment, and reencountered fish with individual identification of tags. The second phase of the experiment also commonly encompasses several sampling occasions with equally thorough compilation of information, including the number of primary tags lost. However, in spite of this richness of data, a Petersen estimator pools tagged fish into a single group regardless of their encounter histories, and recoveries into another regardless of their recovery dates (although stratification practices are common, usually separating the run into three main groups, females, males, and jacks; spatial stratification is also applied in some studies coping with large and complex systems). These pooling methods do not represent a major problem when following a two-sample, closed-population approach where all relevant assumptions (see Box 1) are defensible, but

represent major bias sources when these assumptions are violated (Schwarz and Taylor 1998, Kendall 1999).

The richness of information commonly generated by well-planned mark-recapture studies is not thoroughly used under a standard Petersen protocol, therefore missing important opportunities to enrich our knowledge of salmon ecology. In the last 25 years important developments in capture-recapture analysis have taken place; however, the appreciation many practicing biologists have for modern methods lags behind these recent mathematical, statistical, and computational developments (Amstrup et al. 2005). For instance, in the 2009 Atnarko mark-recapture experiment, 4 304 fish were encountered in 33 sampling occasions over a 47-day period with the first 15 occasions encompassing the tagging period. This richness of information is rarely seen in mark-recapture experiments in vertebrate populations. It is therefore argued that such an effort should be capitalized on by applying modern methods and following an experimental approach characterized by the evaluation of closure assumptions, mark-recapture model selection, and the optimization of the use of information. Regarding the last point, the present report includes the use of the Atnarko 2009 mark-recapture data to generate residence times (required for area under the curve estimates of population size) and migration phenologies that could shed new light into salmon reproductive ecology.

1.5 Objectives

In spite of 2009 being the first year in which modern mark-recapture methods are used in the Atnarko, capture logbooks designed for the Petersen method, as used in previous years, were considered appropriate for the application of modern techniques but required additional data-management work to generate the individual encounter histories upon which modern techniques operate. However, the transition from the standard data compilation to the new scheme could have had a cost in terms of the thoroughness to record recaptures and losses-on-capture (i.e., removals and incidental mortality), which are important in any mark-recapture experiment but particularly in those based on individual encounter histories. In addition, under a double-tagging scheme tag loss can have a larger influence in the estimation process based on individual encounter histories than in a process based on two samples (e.g., Petersen estimate). For these two reasons, the Petersen estimator is included in this report and its results contrasted with those of alternative models. At the end, all the evidence gathered in the experiment is interpreted in light of the assumptions and hypotheses associated to specific models and the ecology of Atnarko Chinook salmon and the quality of information attained for the corresponding analyses.

The main goals of this paper are: (i) to provide an estimate of the 2009 Chinook salmon spawning escapement in the Atnarko River applying the standard Petersen mark-recapture experiment; (ii) to introduce a robust approach to spawning escapement estimation within a model selection framework encompassing suites of open-population and closed-population maximum likelihood estimators and formal testing of primary closed-population assumptions; and, (iii) to demonstrate the use of information provided

by individual encounter histories from mark-recapture experiments, allowing the reconstruction of migration phenologies and the estimation of stream residence times.

Box 1. Closure definition

Closure means that the size of a population is constant over the period of investigation: no additions (birth or immigration) or losses (death or emigration) occur. A closed population is one that does not change composition during the course of the study. This is a strong assumption and difficult to be completely true in a biological population. In general, closure means that there are not **unknown** changes to the initial population. In practice, this means known losses (sampling deaths or deliberate removals) do not violate our definition of closure. If a study is properly designed, closure can be met, at least approximately. Further, the closure concept can be subdivided into two components: geographic and demographic. Geographic closure is due to a boundary limiting population dispersal whereas demographic closure refers to closure to additions and losses. This distinction is important because open models are open to demographic closure, but geographic closure is still a critical assumption (White et al. 1982).

Following the description of sampling and marking protocols, the construction of encounter histories, and the treatment of lost tags, the sequence of tests and analyses is described in six steps. First, the Petersen estimation procedure was separately applied to females, males, and jacks (precocious males with POH lengths under 580 mm). Stratifying by sex can reduce the influence of heterogeneity in survival and capture probabilities (Arnason and Mills 1981; Pollock et al. 1990). Second, a test for demographic closure (Stanley and Burnham 1999) was conducted at two levels, one including carcass recoveries and one without them. Third, a model selection approach was applied to 21 open-population models (Schwarz and Arnason 1996) resulting from combinations of various assumptions pertaining to capture probabilities, survival rates, probabilities of entering the system at different times, and stratification by sex (female, male, jack). Model selection was complemented with goodness-of-fit tests. Fourth, model selection and goodness-of-fit tests were also applied to six close-population models resulting from combinations of assumptions pertaining to capture and recapture probabilities and stratification by sex. The evaluation of closed-population models was separately conducted for maximum likelihood estimators (MLE) developed by Otis et al. (1978) and Huggins (1989). Fifth, based on the best open-population model, separate migration phenologies of females, males, and jacks were constructed to provide information that could enrich our knowledge on salmon reproductive ecology. Finally, residence times of females, males, and jacks were computed following the method developed by Manske and Schwarz (2000).

2. METHODS

2.1 Sampling and marking

2.1.1 Tag application

Double tagging was used to mark Atnarko Chinook. Kurl-lock Ketchum tags (<http://www.ketchum.ca/>) were used as primary marks while operculum punches were utilized as secondary mark. The Atnarko was divided into 6 reaches, with divisions based on accessibility to the river, historical evidence of spawning similarity, and ability to drift reach in a single day. The reaches were assigned designations 1 to 6 starting with 1 at the uppermost section of the sample swath of river. The primary methods used for capturing Chinook included both gill netting and seining, which were specifically targeted to different sections of the river. Multiple crews were usually present on the Atnarko River for each day of the experiment. Gill netting was performed due to inaccessibility and substrate containing large debris while seining was used in specific pools under the condition that too many fish were holding to be successfully gill netted. Also it should be noted that gill nets, though excellent for capturing adult fish, can be slightly less suitable for catching jacks, unlike the seine method which has no selectivity for fish size. Fish were individually marked and released. Releases of tagged specimens were performed so as to avoid re-capture in the same sampling event, and in the rare event that a fish was noticed to have slight difficulty remaining upright, it was carefully held until it swam away of its own volition.

Three unique operculum punch scenarios were used during the mark recapture experiment. Fish captured in the upper section of the sample area (reaches 1 and 2) were given one punch on their right operculum, fish captured in the middle section (reaches 3 and 4) were given 2 punches on their left operculum, while fish in the lower section (reaches 5 and 6), received one punch on their left operculum. Tags were applied several inches above the bottom of the right operculum, so as to avoid tag loss due to fish digging the redds which might occur if the tag were applied at the bottom of the operculum. Care was taken to ensure that Ketchum tags were crimped properly, and in the event that a tag was improperly secured it was retired. Tags were not re-used if they became improperly crimped.

To properly reflect the population distribution on the river, an effort was made to sample fish at a river breakdown of 40%, 20%, and 40% for the upper, middle, and lower sections, respectively. These percentages are based largely on drift counts conducted before the experiment began and historical evidence of Chinook holding patterns before spawning occurs. The actual ratios of fish tagged during the mark-recapture experiment were 40.6%, 18.6% and 40.8%, for the upper, middle and lower sections, respectively, which is in good agreement with the projected targets. From the 925 successfully tagged, 31.24% were females, 13.30% jacks, and 55.46% males. This disparity can be explained by the fact that seining could not be performed often in the upper and middle river sections due to water level, therefore fewer jacks were captured (the seine net used had much smaller mesh than the gill net).

2.1.2 *Carcass recovery*

The deadpitch of carcasses was initiated following the discovery of the first dead fish on the river. Deadpitch crews consisted of one diver, at least one boatman and up to two or more spotter/ shore walkers. Divers were equipped with a gaff hook, while shore walkers typically used a pew to carry carcasses. On occasion, in pooled regions that were too deep for divers to successfully retrieve carcasses by free diving alone, jigs were also employed. Multiple crews were switched between all reaches of the river to minimize any bias in looking at different locations where carcasses build up. During the primary die-off following the spawning peak, three crews were sent to the river, so as to check every reach during every second sampling event. This ensured that there were only minimal losses from fish being missed. As the number of carcasses decreased, the number of crews was decreased accordingly, until only one crew was utilized on the last week of the dead pitch.

Carcasses were examined for sex, primary and secondary marks, and adipose clipped fins (AFC). The presence of AFC indicates that the fish was of hatchery origin and probably with an inserted coded wire tag (CWT). In the case of AFC fish, POH length was recorded, five scales were taken, and the head was removed and E-tagged for proper storage until CWT could be read. Random biological sampling of the wild population was also undertaken, consisting of POH measurement and five scale samples. A target of 800 fish was initially set to ensure statistical robustness, and a limit was placed on the number sampled per day (a target of 30 sampled carcasses was set) however once the target was met additional samples were taken to ensure that the subsequent statistical distribution was representative of the population of the entire run. Effort was made to sample fish with uniform spatial randomness, as different sections of the river tend to accrue different genders (for instance females tended to die closer to their spawning redds).

All fish were recorded and then disposed of according to location on the river. At river locations away from easy human access, carcasses were simply placed above the high water mark on the river bank, so as to avoid being re-washed into the river (in many cases this resulted in fish being placed in the forest adjacent to the river). In areas easily accessible to the public, the tails of fish were cut off, and the carcasses returned to the river.

2.1.3 *Biosampling*

Scale samples and length measurements were collected from 966 carcasses. Scales were placed in a labelled plastic envelope and the individual scales from each fish were mounted in scale books in the field. Ageing of scales was conducted at the DFO scale laboratory in Vancouver BC. In addition, a portion of adipose-clipped fish (CWT) was sampled for age (CWT decoding). Heads were removed from adipose-clipped fish and saved for CWT extraction and decoding at the coded-wire tag dissection laboratory in Nanaimo BC. Ageing data were accepted on the premise that the scales contained a

portion of the previous annulus and were not regenerated. Scales were rejected at the ageing lab if they were mounted upside down, if they were resorbed, or if they had regenerate centers. Ages were recorded for fish where at least two scales could be read for both marine and freshwater ages. The ageing system in this report follows the method originally described by Gilbert and Rich (1927). For the purposes of this report only the total age was reported. The population of each age class was then determined by allocating portions of spawning escapement estimates to age classes according to the age composition determined from scale samples.

2.1.4 *Encounter histories*

In the 2009 Atnarko mark-recapture experiment, fish were encountered in 33 sampling occasions over a 47-day period (August 23 – October 8) with the first 15 occasions encompassing the tagging period and with sampling intervals (elapsed time in days; interval) distributed as follows: (1; _), (4; 3), (5; 1), (6; 1), (7; 1), (8; 1), (11; 3), (2; 1), (13; 1), (14; 1), (15; 1), (19; 4), (20; 1), (21; 1), (22; 1), (23; 1), (25; 2), (26; 1), (27; 1), (28; 1), (29; 1), (32; 3), (33; 1), (34; 1), (35; 1), (36; 1), (39; 3), (40; 1), (41; 1), (42; 1), (43; 1), (46; 3), (47; 1).

During the experiment, 925 fish were tagged (some of them recaptured alive once or more times or recaptured dead once), 969 fish were removed from the system for hatchery purposes, and 2 630 carcasses were recovered of which 220 were tagged. Due to unresolved tags and tagged fish taken to the hatchery and returned at a latter date, a total of 4 273 encounter histories were available and suitable for analyses (Table 1). Although a spatial stratification of the Atnarko (lower, middle, and upper) was employed for data collection, the existence of recaptures in one section of fish tagged in other sections suggested the elimination of spatial stratification as a sound approach. Encounter data compiled during the experiment were formatted as individual encounter histories (see Appendix E for the construction of encounter histories) and using two temporal stratification and recovery schemes. The tabulation scheme 902-15 represents the 902 resolved tagged fish encountered in the 15 occasions representing the tagging period, which was distributed across the first 22 days of the experiment.

The second tabulation scheme, 4273-5, included not only tagged fish but also fish removed for hatchery purposes and untagged fish recovered during the carcass-recovery period. Carcass recoveries were recorded as losses-on-capture (Schwarz et al. 1993). Encounters were stratified in 5 sampling occasions with the first four encompassing 8-day periods and the last occasion encompassing a 15-day period. Avoiding model overparameterization was the main reason of pooling sampling occasions in the 4273-5 scheme. The number of model parameters can be extremely large when stratifying by sex and under 33 sampling occasions with sampling variances increasing with the number of model parameters (Nichols 1992). Other reasons for these tabulation schemes will become obvious in the next sections

2.1.5 Tag loss

A novel approach to the treatment of lost tags in double-tagging experiments is herein introduced. A high tag-loss rate of 23.8% (36.7% in females, 17.5% in males, and 19.5% in jacks) was treated through a stratified random redistribution of primary tags at risk among recovered fish possessing only secondary marks. More specifically, a reconstruction of individual encounter histories was possible thanks to the presence of secondary marks that allowed the random redistribution of marks at risk among recovered individuals possessing only secondary marks. Marks at risk are represented by all individuals that have been previously tagged and assumed to be available for recapture based on their encounter histories. The random distribution of tags among recovered fish possessing only secondary marks respected the group affiliations: females, males, and jacks. This stratified random distribution of tags at risk was conducted using randomization procedures with the aid of the computer software MATLAB version 7 (The Mathworks Inc, Natick, Massachusetts).

2.2 Analyses

2.2.1 Petersen estimate

The adult Chinook salmon spawning escapement was estimated using the modification of the Petersen estimator proposed by Robson and Regier (1964). In anticipation of significant sex related differences in the data, and in order to facilitate comparison with past or similar studies, the escapement (N_g) was computed separately for males, jacks, and females as:

$$N_g = \frac{(M_g + 1)(n_g + 1)}{m_g + 1} - 1 \quad (1)$$

and its standard error (SE_g) as:

$$SE_g = \sqrt{\frac{(M_g + 1)(n_g + 1)(M_g - m_g)(n_g - m_g)}{(m_g + 1)^2 (m_g + 2)}} \quad (2)$$

where M_g is the number of fish released with primary and secondary marks, m_g is the number of primary and/or secondary marked carcasses recovered, and n_g is the number of carcasses examined for marks. Subscript g refers to the sex group (females, males, or jacks).

2.2.2

Bias assessment

Previous mark-recapture experiments of Pacific salmon spawning escapement have conducted tests for sampling selectivity (e.g., Chamberlain and Parker 2007, Tisdale et al. 2007) to assess violations of the basic assumptions around the pooled-Petersen estimation method. In the present study, analytical procedures for the evaluation of bias in sampling selectivity associated to time period, location, and sex (i.e., females, males, jacks) were explicitly incorporated into the modelling process (see Sections 2.2.5 and 2.2.6). Differences in probability of capture, probability of survival, probability of entrance, and probability of recapture between sampling events were part of the analyses and examined through goodness-of-fit tests, likelihood-ratio tests, and model selection (see next sections). In addition to an explicit stratification by group (males, females, and jacks), differences in sampling selectivity between groups was assessed through goodness-of-fit tests (see section 2.2.4.1).

Size-related bias in the application of tags was assessed by comparing the POH length frequency distributions of tagged and untagged carcasses with the Kolmogorov-Smirnov two-sample test. This statistical test assesses the hypothesis that two samples were drawn from different populations. Unlike the t-test or the Mann-Whitney test, which test for differences in the location of the two samples (e.g., means and ranks, respectively) the Kolmogorov-Smirnov two-sample test is also sensitive to the general shapes of the distributions in the two samples (Sokal and Rohlf 1981).

Ventral compression was applied to 533 female carcasses (82% untagged and 18% tagged) to investigate whether individuals died after or before spawning. Bias associated with pre-spawning mortality linked to tagging and handling the fish was analyzed by a simple chi-square test. The evaluation of this source of bias in males is not feasible from the observation of gonads in carcasses. Tagging stress in males and females has been assessed in other studies by comparing the rates of mark recovery associated with various release conditions categories defined by bleeding levels or injuries (e.g., Tisdale et al. 2007).

2.2.3

Closure test

The closure test for time-specific data developed by Stanley and Burnham (1999) was used to test the null hypothesis of closed-population model M_t against the open-population Jolly-Seber model. The closed-population model M_t corresponds to a model where the probability of capture and recapture vary with time but the two are identical in any given sampling occasion. The closure test is a chi-square test that can be used to determine the nature of closure violations, namely, unknown additions or/and losses to the population during the study period. Computer software Close Test Version 3 (T.R. Stanley and J.D. Richards, USGS, Fort Collins Center, Colorado) was used to test for closure under the two tabulation schemes. The test component for losses should indicate violation to closure owed to losses under the 4273-5 scheme due to the recovery of dead

individuals but not necessarily under 902-15. However, the test component for additions could indicate violation to closure under both schemes.

2.2.4 *Model selection procedure*

The mark-recapture analyses of 2009 spawning escapement from the Atnarko River followed a model selection approach as described in Lebreton et al. (1992), which encompasses the following steps:

- 1) Start from a global model compatible with species biology and assess its fit
- 2) Use goodness-of-fit tests of the global model
- 3) Select a more parsimonious model using Akaike's Information Criterion (AIC) to limit the number of formal tests
- 4) Compare parsimonious model with neighbouring models using likelihood ratio tests (LRT)
- 5) Obtain maximum likelihood estimates of model parameters, including precision

These steps were separately applied to both, open-population and closed models. Program MARK (Gary C. White, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado) was used for AIC model selection and derivation of MLEs.

2.2.5 *Open-population models*

The generalization of the Jolly-Seber model using a multinomial distribution from a super-population (i.e., the total number of animals that are ever available for capture in the population of interest over the course of the study), as described by Schwarz and Arnason (1996; see Box 2 for a summary of statistics, parameters, and functions), was applied to 21 models fitted to data from tabulation scheme 4273-5 further stratified by sex (females, males, and jacks). These models were defined by their explicit assumptions about the main probability components of the likelihood estimation: capture (p), survival (ϕ), and recruitment (i.e., entrance to the study area) (b). The importance of differentiating probability components between groups was also part of model construction. Estimation bias due to heterogeneity in survival, capture, and recruitment can be minimized by stratifying the data (e.g., by sex; Arnason and Mills 1981). This modelling framework facilitates the incorporation of constraints (e.g., equal survival per time period), is not affected by unequal time intervals between sampling occasions, and covariate models on any scale can be easily incorporated.

In the super-population model, the likelihood function of the mark-recapture experiment is partitioned into three components:

$$L = L_1 \times L_2 \times L_3 = P(\text{first capture} \mid p_i, \phi_i, B_i) \times P(\text{losses on capture} \mid v_i) \\ \times P(\text{recapture} \mid p_i, \phi_i) \quad (3)$$

Box 2. Summary of statistics, fundamental parameters, and functions of parameters used in the Schwarz and Arnason (1996) open-population mark-recapture methodology

Statistics

n_i	Number of animals captured at occasion i , both marked and unmarked. $n_i = m_i + u_i$.
u_i	Number of unmarked animals captured at occasion i .
m_i	Number of previously marked animals captured at occasion i .
R_i	Number of animals released alive at occasion i , i.e., just after sampling occasion i .
r_i	Number of animals from R_i that are subsequently captured after occasion i .
z_i	Number of animals seen before i , seen after occasion i , but not seen at occasion i .
l_i	Losses-on-capture are found as $n_i - R_i$

Fundamental parameters

k	Number of sample times
p_i	Probability of capture at sample time i
ϕ_i	Probability of an animal surviving and remaining in the population between sample occasions i and $i + 1$ given it was alive and in the population at occasion i
B_i	Number of animals that enter after sample time i and survive to sample time $i + 1$. B_0 is defined as the number of animals alive just prior to the first sample time
N	Total number of animals that enter the system and survive until the next sample time. $N = B_0 + B_1 + \dots + B_{k-1}$
b_i	Fraction of the total additions to the system between sample times i and $i + 1$. These are referred to as the entry probabilities $b_i = B_i/N$
v_i	Probability that an animal captured at time i will be released

Functions of parameters

N_i	Population size at time i . $N_i = B_0$; $N_{i+1} = (N_i - n_i + R_i) \phi_i + B_i$
U_i	Number of unmarked animals in the population at time i . $U_i = 0$; $U_{i+1} = U_i(1 - p_i) \phi_i + B_i$
B_i^*	Gross number of animals that enter between sampling occasions i and $i + 1$. These include animals that enter and die before the next sampling occasion

According to this formulation, the only recoverable information on capture and survival rates is found in the recaptures of previously marked individuals, the relative proportions of unmarked individuals captured gives information about the relative number of new additions, and the total number of unmarked individuals gives information about the total population size (see Schwarz and Arnason 1996 for a full definition of likelihood components and maximization procedures). The delta-method is used to obtain estimates of the variances and covariances for functions of model parameters.

In the open-population model developed by Schwarz and Arnason (1996), injections (i.e., births or immigration) and losses (i.e., deaths or emigration) can occur at any time during the experiment, the number of individuals present just prior to the first sample occasion (B_0) can be estimated, and the gross number of animals that enter between sampling occasions i and $i + 1$ (B_i^* ; these include animals that enter and die before next sampling occasion) can be differentiated from the number of animals that enter after sample time i and survive to sample time $i + 1$ (B_i). The term B_i^* is of interest when estimating a salmon spawning population size as it refers to the total escapement from the fishery that returns to spawn (Schwarz and Arnason 1996).

2.2.5.1 Goodness-of-fit

Differences in survival and capture probabilities of individuals within each group (females, males, and jacks) within sampling intervals and differences in survival and capture probabilities among groups were assessed with chi-square tests following the protocol provided by Burnham et al. (1987) and using the computer program RELEASE (Gary C. White, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado). In this protocol, Test 1 assesses differences in both capture and survival probabilities among groups, Test 2 assesses individual capture probabilities, and Test 3 assesses individual survival probabilities.

Likelihood-ratio tests (LRT) were conducted using MARK applications to test for significant differences between neighbouring models. The difference in deviance between 'nested models' (models in which one model differs from another by the elimination of one or more model terms) is distributed as a chi-square statistic with the degrees of freedom given as the difference in the number of estimable parameters between the two models. This forms the basis of the LRT and it is included herein to complement the results of the AIC model selection.

2.2.5.2 Estimating spawning escapement

If escapement is defined as the number of fish that escape marine and terminal fisheries and return to a river to spawn, an estimate of escapement will include the fish that enter the system but die before spawning. However, it is important to estimate the number of fish that actually survive to become potential spawners. Jolly-Seber treatment

of additions estimates the number of animals that enter the population after a sampling occasion and are alive at the next sampling occasion. Such estimates therefore exclude the animals that enter the system but die before the next sampling occasion. These Jolly-Seber estimates would underestimate the true abundances, except when all animals survive from their entry to the next sampling occasion (Schwarz et al. 1993). Modifications to the Jolly-Seber allowing estimates of the total number of fish returning to a river, including those that die between sampling occasions, have been developed by Schwarz et al. (1993) and incorporated into MARK to allow the computation of both gross and net population estimates. The gross estimates include the number of individuals that die during the mark-recapture experiment and are unaccounted for in the records of losses-on-capture.

Given that the sampling period incorporates a carcass-recovery phase, the super-population size derived from 4273-5 ($\tilde{N}_{4273-5}$) was multiplied by the net-to-gross population size ratio from the 902-15 encounter history scheme (R_{902-15}) to estimate the spawning escapement ($S = \tilde{N}_{4273-5} R_{902-15}$). Given that fish removed from the system for hatchery purposes had also encounter histories represented in data scheme 4273-5, there is no need to subtract their number from the effective number of natural spawners. This procedure was applied separately for females, males, and jacks.

2.2.6 Closed-population models

The evaluation of closed-population models was separately conducted for maximum likelihood estimators developed by Otis et al. (1978) and the more recent approach developed by Huggins (1989). The reader is referred to Chao (2001) for a recent review and general theory. The main difference between these two approaches is that the Otis et al.'s model includes abundance in the likelihood whereas the Huggins' model leaves abundance condition out of the likelihood. The primary advantage of the Huggins' approach is that individual covariates can be used in the modelling. Model selection followed the steps described for open-population models and applied to 6 models fitted to data from tabulation scheme 4273-5 further stratified by sex (females, males, and jacks). These models were defined by their explicit assumptions about the main probability components of the likelihood estimation: probability of capture (p) and probability of recapture (c). The importance of differentiating probability components between groups was also part of model construction.

The likelihood for closed-populations is defined as:

$$\mathcal{L}(f_0, p, c | data) \propto \frac{(f_0 + M_{t+1})!}{f_0!} \prod_h \text{Pr}[h]^{n_h} \cdot \text{Pr}[\text{not encountered}]^{f_0}. \quad (4)$$

where M_{t+1} is the number of unique animals marked (i.e., marks at risk), f_0 is the number of individuals never caught, $f_0 = N - M_{t+1}$, and n_h is the number of individuals with encounter history h . Therefore,

$$\hat{N} = \hat{f}_0 + M_{t+1} \quad (5)$$

and

$$\text{var}[\hat{N}] = \text{var}[\hat{f}_0] \quad (6)$$

2.2.7 Hatchery contribution

Juvenile Atnarko Chinook have been adipose fin clipped and marked at the Snootli Hatchery with either binary coded-wire tags as described by Jefferts et al. (1963) or decimally coded-wire tags using standard methods (Armstrong and Argue 1977). The latter is currently conducted at the Snootli hatchery.

All adipose-fin-clipped fish deadpitch recoveries were sampled for scales and heads taken for CWT reading. Estimates of the contribution of hatchery-reared Chinook to the total escapement were calculated by expanding the percentage of CWT's in escapement counts by tag code (Kuhn 1988). The number of successfully decoded CWT Chinook in the escapement was estimated and stratified by age and sex. Estimating the total number of CWT returns from each of the brood years, and for each tag code, was done as follows.

First, the observed number of CWT recoveries was adjusted to account for "no pin" (adipose clipped but no CWT in nose) recoveries:

$$ADJ_{i,tc} = OBS_{i,tc} \left[1 + \frac{LP_i}{K_i} + \frac{ND_i(K_i + LP_i)}{K_i(K_i + LP_i + NP_i)} \right] \quad (7)$$

where $ADJ_{i,tc}$ is the adjusted number of observed CWT fish for a particular tag code within a stratum, $OBS_{i,tc}$ is the observed number of CWT fish, K_i is the sum of all successfully decoded tags for all tag codes recovered in a particular stratum, LP_i is the number of lost pin recoveries, ND_i is the number of no data recoveries, NP is the number of no pin recoveries, and i and tc are the subscripts denoting stratum (i.e., female, male, jack) and tag code, respectively. This adjusted number of CWT recoveries was then be used to estimate the total number of CWT returns for each tag code:

$$EST_{i,tc} = \frac{ADJ_{i,tc} P_i}{C_i} \quad (8)$$

where $EST_{i,tc}$ is the estimated number of CWT recoveries for a single tag code within a stratum, C_i is the number of fish examined (carcasses recovered in this case), and P_i is the population estimate for stratum i . Note that the sum of $EST_{i,tc}$ values for all tag codes in a particular stratum represents the number of hatchery-marked fish in the spawning escapement.

The hatchery contribution to escapement, stratified by sex, was calculated by expanding the estimated number of CWT fish of each tag code group in proportion to the percentage of juvenile fish having a CWT at time of release:

$$EHC_{i,tc} = \frac{EST_{i,tc}(RM_{tc} + RUM_{tc})}{RM_{tc}} \quad (9)$$

where EHC is the estimated hatchery contribution, RM is the number of Chinook released with CWTs for each tag code group (tc), and RUM is the number of Chinook released without CWTs for each tag code group (tc). The term $EHC_{i,tc}$ represents the expanded recoveries, which are the estimated number of fish represented by a particular tag code recovered in a stratum, including marked and unmarked hatchery fish.

These estimates of hatchery contribution by tag code were then summed to give the hatchery contribution of all tag codes to the entire escapement, stratified by sex and brood year:

$$EHC_{i,t} = \sum_{t=1}^j \sum_{i=1}^m \sum_{tc=1}^n EHC_{i,j,tc} \quad (10)$$

where n is the number of tag codes for a given brood year t .

Percent hatchery contributions by sex and age were then calculated using the best population estimates for adult males, jacks, and females.

2.2.8 Spawning run phenologies

One of the advantages of the open-population approach (when applicable) is the derivation of B_i^* , the number of fish that enter the system after sampling occasion $i+1$ ($i = 0, \dots, s-1$, with s referring to the number of sampling occasions), and the generation of probabilities of entering the system at each sampling occasion (b_i). For the analysis of entry probabilities we used scheme 902-15 because the inclusion of carcass recoveries generates high capture rates (capture probabilities increased substantially during the carcass recovery) in the last sampling interval, producing the false impression of a largest b at the end of the experiment. Therefore using scheme 902-15 eliminates this confounding effect and in addition allows for a greater temporal resolution due to the larger number of sampling points (15).

The construction of spawning run phenologies was conducted separately for females, males, and jacks. A cumulative-frequency approach was developed entirely on the basis of scheme 902-15, and an absolute-abundance approach was developed by combining the b_i values derived from 902-15 with the group abundances derived from 4273-5.

2.2.9 Stream residence time

The average stream residence (R) is the average time that a fish spends in the system under study. An individual fish arriving t units (t_i represents the time interval from sampling occasion i to sampling occasion $i + 1$) after sampling occasion i has a $\phi^{(1-t/t)}$ probability of surviving until the next sampling occasion and contributes $(t_i - t)$ time units to the aggregate residence time (Manske and Schwarz 2000). Hence residence time can be also interpreted as the average length of time that fish (in some cases within a particular group) are associated with a particular area and potentially available for sampling.

Stream residence times were computed separately for females, males, and jacks using scheme 902-15 and applying Manske and Schwarz's (2000) model (equation 12), which uses parameters derived from the open-population multinomial model developed by Schwarz and Arnason (1996).

$$\hat{R} = \left\{ 0.5 \sum_{i=1}^{s-1} t_i \hat{N}_i^+ (\hat{\phi}_i + 1) + 0.5 t_s \hat{N}_s^+ + 0.5 \hat{B}_0 t_0 \right. \\ \left. + \sum_{i=1}^{s-1} \hat{B}_i t_i \left(\frac{\hat{\phi}_i}{\hat{\phi}_i - 1} - \frac{1}{\log \hat{\phi}_i} \right) \right\} / \left(\hat{B}_0 + \sum_{i=1}^{s-1} \hat{B}_i^* \right) \quad (12)$$

where N_i^+ is the number of fish alive in the system immediately after sampling occasion i , ϕ_i is the survival probability between sampling occasion i and $i+1$, s is the number of sampling occasions, t_i is the length of the interval from sampling occasion i to $i+1$ (assume $t_s = t_{s-1}$) and B_0 , B_i , and B_i^* as defined before.

3. RESULTS

3.1 Petersen estimate

With an overall recapture rate of 23.8%, the pooled-Petersen procedure estimated 3 593 (95% CI: 3 077-4 108) females, 5 637 (95% CI: 4 640-6 632) males, and 1 532 (95% CI: 1 028-2 035) jacks for a total escapement of 10 761 (95% CI: 8 745-12 775). The coefficient of variation (CV) was 7.3%, 9.0%, and 16.7% for females, males, and jacks, respectively, and 5.7% for the entire population. These estimates do not account for those fish removed from the system for hatchery purposes (969).

3.2 Size-related bias

The analysis of length frequencies of tagged and untagged carcasses indicated there were no significant differences in location or shape of frequency distributions of the two samples (Kolmogorov-Smirnov two-sample test: $p < 0.01$). Mean sample length was 684.4 mm in tagged fish and 684.2 in untagged fish while the standard deviations were 84.3 mm and 84.6 mm in tagged and untagged fish, respectively. This analysis indicated there was not size-selectivity in sampling and tag application with the potential to cause bias in escapement estimates.

3.3 Tag-mortality bias

From 533 female carcasses sampled for egg retention, 109 were tagged and 424 untagged. Twelve (2.4% of the sample) female carcasses (1 tagged, 11 untagged) exhibited egg retention in the range 25%-100%. For the purposes of this analysis, all levels of egg retention were grouped together. The chi-square test ($\chi^2_{0.05, 1} = 3.841$; $\chi^2_{\text{contingency table}} = 1.11$; $P > 0.25$) indicated that egg retention, here used as an indicator of pre-spawning mortality, was not independent of tag status. However, the results of the test said nothing about potential effects of tagging on pre-spawning mortality because 92% of the female carcasses exhibiting egg retention were untagged. More specifically, tagged fish did not exhibit greater levels of pre-spawning mortality relative to untagged fish; the difference between strata is most likely a random effect caused by the small sample size ($n = 12$).

3.4 Closure test

The outcome of the closure test indicated failure of closed-population assumptions for additions and losses in both, 902-15 (Table 2) and 4273-5 (Table 3) data schemes.

3.5 Open-population models

Goodness-of-fit tests indicated significant differences in survival and capture probabilities between groups (Test 1: Chi-square=52.8204; $df=12$; $P<0.0001$), and no-significant differences in individual survival (Test 3) or capture (Test 2) probabilities within consecutive sampling occasions for either females (Chi-square=8.31; $df=7$; $P=0.306$), males (Chi-square=9.47; $df=7$; $P=0.220$), or jacks (Chi-square=1.87; $df=6$; $P=0.479$). In other words, goodness-of-fit tests did not detect any serious evidence of failure of the assumptions of equal catchability or survival (i.e., the homogeneity assumptions) among individuals of a given group within a sampling period but differences between groups were found.

Open-population models are defined by the probability of capture (p), the probability of survival (ϕ), and the probability of recruitment (i.e., entering the system) (b) under time-specific (t), group-specific (g), time- and group-specific (g^*t), and/or invariant (*) conditions. Only 19 of the 21 models assessed appear in the AIC's model selection (Table 4) because models $\{p(g), \phi(t), b(g)\}$ and $\{p(g), \phi(g^*t), b(g)\}$ did not converge. Models including time varying capture probabilities $p(t)$ or $p(g^*t)$ were not included in the list because they have unidentifiable parameters that generate unreasonable parameter values (Amstrup et al. 2005). Based on the AIC weights, the best model corresponded to $\{p(g), \phi(*), b(g^*t)\}$, which indicates differences in capture probabilities between groups, time-invariant survival probabilities and both time-specific and group-specific differences in entry probabilities (see Table 5 for results of the best model). Further, the fact the models with $b(g^*t)$ were at the top of the AIC ranking can be considered as another piece of evidence against the closure assumptions. Although LRTs were not informative because of lack of model nesting, the three best models (which include $b(g^*t)$) generated identical population parameters. Best open-model escapement estimates were 8 232 (SE: 615.2) females, 7 877 (SE: 513.2) males, and 4 159 (SE: 796.5) jacks for a total escapement estimate of 20 268 (95% CI: 16 985 – 24 601; CV = 9.5%). These numbers represent the fish escaping the terminal fisheries and entering the study area, and include the fish removed for hatchery purposes. Accounting for the survival rates of Chinook salmon within the study period, as derived from data scheme 902-15 (0.95 for females, 0.94 for males, and 0.95 for jacks) leaves a total of 19 157 effective natural spawners.

3.6 Closed-population models

Closed-population models are defined by the probability of capture (p) and the probability of recapture (c) under time-specific (t), group-specific (g), time- and group-specific (g^*t), and/or invariant (*) conditions. Six models were compared under the AIC framework but only five appear in Table 6 because model $\{p(g), c(g)\}$ did not converge. Best model, $\{p(g^*t)=c(g^*t)\}$, was consistent with the findings of the open-population experiment, namely, probability of capture is group-specific. However, this model includes capture probabilities varying with time (Table 7). This best model is a general form of the M_t model used as null model in the test for closure (Stanley and Burnham 1999). In other words, this was the model rejected in the test given the evidence against demographic closure. In addition, capture probabilities derived from the best closed-population model show capture probabilities in the last sampling interval (carcass recovery) that are an order of magnitude greater than the previous intervals for all three groups. This substantial increase in capture probabilities produces an underestimation of abundance for each of the groups in the analysis. Likelihood ratio tests (Table 8) were successful to identify the best model as significantly different from its nested models. These results were similar using either Otis et al.'s (1978) or Huggins' (1989) approach.

Population sizes generated with the best closed-population model were 10 925 (4 202 (SE: 260.8) females, 4 714 (SE: 269.0) males, and 2 009 (SE: 357.4) jacks) for a total escapement smaller than the one obtained with the best open-population model (20,268).

However, the best closed-population model indicated capture probabilities varying with time. A comparison of a closed-population model compatible with the best open-population model (i.e., $p(g)=c(g)$) shows similar total population size (20 242) but differences in the group contributions to total population size (10 292 (SE: 798.3) females, 6 680 (SE: 416.1) males, 3 270 (SE: 614.7) jacks).

3.7 Age-specific spawning escapement

Scales from 996 Chinook carcasses were taken to the laboratory. Scales from 272 fish were partially read and 44 were unreadable. Therefore, successful ageing of scales was conducted for 680 individual fish. This analysis indicated that 12.5% of individuals in the sample corresponded to age-3 fish, 49.6% to age-4, 36.9% to age-5, and 1.0% to age-6 fish. The analysis of freshwater versus marine annulus indicated that 72% of the sample corresponded to ocean-type fish while 28% corresponded to stream-type fish. At the age-specific level, 100% of the age-3 fish and 91.4% of the age-4 fish exhibited ocean-type life history whereas only 37.9% of the age-5 fish and 28.6% of the age-6 fish exhibited this life history type.

3.8 Hatchery contribution

Adipose-fin-clip incidence rates after adjustment of the numbers of observed CWT fish were 5.04% for females, 8.00% for males, and 13.28% for jacks from a sample of 1 108 carcasses. These rates were determined from 107 heads (39 females, 47 males, and 21 jacks) sampled in the Atnarko, with 95 CWTs decoded (35 females, 42 males, and 18 jacks), one lost head (female), and 11 heads with no pin (3 females, 5 males, and 3 jacks). Eleven tag codes were represented in the sample: 185304 ($n = 17$), 185305 ($n = 14$), 185306 ($n = 21$), 185425 ($n = 6$), 185427 ($n = 12$), 185428 ($n = 15$), 186205 ($n = 4$), 186206 ($n = 3$), 186207 ($n = 1$), 186208 ($n = 1$), and 186209 ($n = 1$). The expansion of these CWT recoveries indicated hatchery contributions of 36.8%, 50.4%, and 61.2% for females, males, and jacks, respectively. This translated into an overall hatchery contribution of 48.7% in the spawning escapement of 2009 Atnarko Chinook. Note that these contributions are independent of the mark-recapture method used to analyze the data.

3.9 Spawning run phenologies

The analysis of spawning-run entry probabilities showed that approximately 27% of the jacks total run was present in the sampling area at the onset of the experiment. Similarly, 18% of the females and 7% of the males were present in the system at the first sampling occasion. But in spite of the proportion of the jack run at the beginning of the experiment being larger than the proportion of females, 94% of the females were present in the system by the third experiment day while jacks reached a similar proportion until

day 11 (Figure 4a). By experiment day 13 all females, males, and jacks in the spawning run were present in the system.

In terms of sheer abundances, the largest flow of individuals into the sampling area ($> 6\,000$) was represented by females during the first 4 days of the experiment (Figure 4b). A second female immigration pulse was detected between days 12 and 14. Immigration pulses of males and jacks were of smaller magnitudes than the first female pulse but they were also spread during the first two weeks of the experiment. Three pulses of similar magnitude characterized the entry of males into the study area whereas only two smaller pulses characterized the jack's run (Figure 4b).

3.10 Stream residence time

The average number of days fish in the 2009 Atnarko spawning run spend in a particular area, becoming available for sampling, differed among females, males and jacks. Females displayed longer residence times (20.3 days) than either males (12.3 days) or jacks (10.7 days). The average stream residence time currently applied to Chinook salmon in the region, 12.8 days (personal communication; Wayne Levesque, DFO Bella Coola, BC), is consistent with our findings for males in the 2009 Atnarko run, and probably for jacks as well, but not with our computed residence times for female Chinook. Together with the analysis of spawning run phenologies, these results indicate that the majority of females arrive earlier than the majority of males and jacks and that their residence associated with particular areas was longer (about twice as much) than either males or jacks. These results also indicate that jacks arrive earlier than males, probably to capitalize on positioning in strategic locations to become competitive spawners, but on average spend less time in association with particular areas.

4. DISCUSSION

4.1 Evaluation of results

The analysis of individual encounter histories indicated that additions to the population during the mark-recapture experiment constituted the main violation to the assumption of closure. Mortality that was not associated with removals for hatchery purposes or post-spawning mortality (i.e., natural mortality unaccounted for) also contributed to the violation of closure. The Petersen estimate of spawning escapement (10 761) was about half of the estimated with the best open-population model. According to the Petersen, 34% of the spawning escapement consisted of females, 52% of males, and 14% of jacks. The best maximum-likelihood closed-population, characterized by time-specific differences in the capture probabilities of each group, estimated a spawning escapement of 10 925, similar to the Petersen estimate. Sex composition was slightly different according to the maximum likelihood closed-population model but the strata ranking was maintained: 39% females, 43% males, and 18% jacks. In contrast, the best open-population model was characterized by differences in capture probabilities between

groups, time-invariant survival probabilities, and both, time-specific and group-specific differences in immigration patterns. According to this model, the spawning escapement was 20 268 fish, from which 41% were females, 39% males, and 20% jacks. Due to pre-spawning natural mortality, 19 157 Chinook were estimated as becoming potential natural spawners.

Although the Petersen estimator has been routinely used to estimate spawning escapement in Pacific salmon, including Atnarko Chinook, fish entering the stream to spawn during the sampling periods violate the closure assumption required by the Petersen (Sykes and Botsford 1986). The pooled-Petersen is consistent and generally unbiased when observable movements are proportional among strata, but its estimate will be biased if the degree of closure is not the same for all release strata (Darroch 1961). Constant or completely random immigration does not introduce bias to estimators from close-population methods, although it decreases precision (Kendall 1999). These two types of immigration do not represent salmon runs in general and Atnarko Chinook in particular. Salmon arrival to spawning grounds is better described as Markovian (dependent on the presence/absence of fish in the previous time periods) with migration phenologies characterized by clear peaks and/or pulses. Simulations have shown that when movement is Markovian, neither the magnitude nor the direction of the bias can be completely predictable (Kendall 1999).

Nevertheless, although closure assumptions did not hold in the 2009 mark-recapture experiment in the Atnarko, large discrepancies in the number of Chinook entering the sampling area after the onset of the experiment existed between those produced by the analysis of immigration rates linked to the best open-population model and fish counts from the Atnarko Tower. This tower is located in the downstream limit of the sampling area and operated 6-24 hours a day during the study (personal communication; Wayne Levesque, Fisheries and Oceans Canada, Bella Coola BC). According to the open-population model, 17 141 Chinook entered the system after the experiment started whereas only 1 006 were estimated from the Atnarko Tower. Even though tower counts are influenced by the experience of counters, environmental conditions, and correction factors for observed time, immigration rates derived from the best open-population model inherently depend on appropriate recording of recaptures and losses-on-capture. Being 2009 the first year that an estimator other than the Petersen has been conducted in the Atnarko River, inconsistencies were identified in the way recaptures and losses-on capture were recorded in field logbooks. Under a Petersen framework, the information provided by recaptures of live fish during the tagging phase is not relevant and therefore easily overlooked in the field. However, this information is crucial in the construction of individual encounter histories and it will influence immigration rates under an open-population framework. If recaptures and losses-on-capture are not recorded at the individual level, an overestimation of immigration rates is granted. This overestimation is also expected to inflate population estimates. Yet, it is intriguing that the spawning escapement estimated by the best closed-population model (which also uses individual encounter histories) was similar to the Petersen estimate.

Consistent with objectives of the present paper, a robust and systematic approach to spawning escapement estimation has been introduced herein as a first step towards the departure from ad hoc approaches in studies characterized by rich sampling efforts. Ad hoc approaches ignore the severe problems associated with count statistics reflecting unknown sampling fractions (Nichols 1992). There are reasons to avoid an ad hoc estimation of escapement other than those mentioned above relating to immigration. A key assumption of the simple pooled-Petersen estimator is that catchability is equal in all tagging strata or all recovering strata. If this is violated, severe bias can occur (Schwarz and Taylor 1998). In salmon populations, capture probabilities can change as a result of changes in fish behaviour, fish readiness to spawn, and environmental conditions. These conditions portray large limitations to the application of the Petersen protocol in salmon studies where catchability rates vary across tagging or carcass recovery and when the degree of closure varies across the tagging period. In the Atnarko 2009 experiment this circumstance was evidenced by the best closed-population model where capture probabilities vary with time. Moreover, an extreme heterogeneity of capture probabilities within fish strata occurs when tagging and carcass recovery periods overlap. This is a common occurrence when trying to achieve a minimum tag application rate as determined by field experience or based on statistical power analysis (Rexstad et al. 1991). In the Atnarko experiment, overlapping occurred between tagging (August 21 – September 17) and carcass recovery (September 11 – October 8) periods.

But in spite of all the reasons given herein to depart from ad hoc approaches, and in spite of the evidence for closure violations, we acknowledge that the open-population estimate from the best model suffered from three important error sources: inconsistent recording of recaptures, inconsistent recording of losses-on-capture, and high tag-loss rates. Both, underreporting of recaptures and losses-on-capture and high tag-loss rates are expected to overestimate the size of the super-population in the open-population model. The two first sources of error can be corrected in future experiments through the use of field logbooks specifically designed for the construction of individual encounter histories and through additional care in the recording of recaptures and losses-on-capture by field crews. In addition, the reintroduction of previously removed fish should be avoided at all cost. Although fish removals can be easily recorded as losses-on-capture, their reintroduction into the system in a later date introduces noise in capture probabilities and therefore affects parameter estimation. The third source of error, tag loss, was treated in the present investigation using randomization procedures. However, future studies should strive to improve of tag-retention rates through the application of better-quality tags and application techniques.

A high tag-loss rate (23.8%) in the mark-recapture experiment of the 2009 Atnarko Chinook spawning escapement was detected with secondary marks. When homogeneous tag loss occurs in a population subject to death but closed to recruitment (as in the carcass recovery phase of the 2009 Atnarko experiment), open-population estimates are expected to overestimate population size (Arnason and Mills 1981). The treatment of these incidences in the present experiment represents only one way of addressing the problem. However, alternative approaches have been described in the relevant literature, based on ad hoc corrections in double-tagging experiments (e.g.,

Arnason and Mills 1981) or through the incorporation of tag-retention parameters into the Jolly-Seber model (e.g., Cowen and Schwarz 2006). Tag-loss correction methods also exist for Petersen mark-recapture experiments with double tagging (Seber and Felton 1981). At any rate, the application of double tags provides unique assistance for statistical inference, and the stratified random distribution of marks at risk implemented in the present study would have not been possible without it. Nevertheless, it remains a challenge to ascertain the degree of bias or the loss of precision still persisting after such treatment of lost tags. Additional studies would be required to test the efficiency of this approach, but the improvement of tagging techniques should not wait. The best way of avoiding estimation uncertainty due to lost tags would be the reduction of tag-loss rates as much as possible.

4.2 Additional information generated by the experiment

The inferences on immigration rates derived from the best open-population model indicated that 18% of the females, 7% of the males, and 27% of the jacks were present in the system at the first sampling occasion, and all fish in the spawning run were within the study area by day 14 of the mark-recapture experiment. For the same reasons provided to interpret with caution the spawning escapement estimate derived from the best-open population model, namely inconsistencies in the recording of recaptures and losses-on-capture, these proportions of fish at the onset of the experiment could be substantially overestimated. However, the end of the immigration period into the study area, 14 days after the beginning of the study, was reasonable and consistent with field observations.

The application of Manske and Schwarz's (2000) method for the estimation of residence times based on data provided by the best open-population model generated stream residence times (in days) of 20.3, 12.3, and 10.7 for females, males, and jacks, respectively. Although the average residence time (14.4 days) is similar to that used in the region for Chinook salmon (12.8 days), the same sources of error adjudicated to the analysis of migration phenologies warn about the interpretation of these results.

Notwithstanding, one of the objectives of the present investigation was to demonstrate the use of mark-recapture data for the derivation of information other than population size. The fact that the use of modern analytical procedures allows for the estimation of survival and immigration rates underpinning the analysis of migration phenologies and stream residence times should motivate the use of mark-recapture experiments that are based on individual encounter histories since they open great opportunities for optimization of both information and cost. Although defined sources of error in the 2009 Atnarko Chinook experiment posed difficulties to the proper interpretation of the results derived from the analysis of individual encounter histories, the identification of these issues is expected to improve significantly the compilation of field data, and therefore the reliability in estimation procedures, in the future.

4.3 Escapement into the Bella Coola watershed

As the majority of Chinook entering the Bella Coola spawn in the Atnarko, the key objective of this paper was to derive a robust estimation of the spawning population of Chinook Atnarko. However, there is also a small group of lower Bella Coola tributary spawners which are enumerated annually using stream walks. These Bella Coola spawners are believed to make up a very small component (~ 300 fish on average) of the overall system. Given that the Bella Coola River Nuxalk Fishery caught 3 729 Chinook in 2009, the number of fish escaping ocean fisheries and commercial net fisheries in the Bella Coola River (see Figure 3) is estimated to be approximately 15 000 when using the spawning escapement produced by the Petersen and the best closed-population model or about 24 000 using the best open-population estimate. Given an interim fisheries management target escapement of 25 000 for Bella Coola Chinook (Pestal 2004), Chinook escapement in year 2009 was most likely below the target. Escapements have exceeded this target in four of the last ten years and have been lower than the target in the past five years (range 15 000 and 24 000; Appendix B).

4.4 Final remarks

The present exercise has demonstrated that it is important to take a systematic approach towards mark-recapture studies designed to provide precise and unbiased estimates of spawning escapement. The main attributes of this approach should include (i) testing for demographic closure, (ii) allowing different hypotheses about the demographic and catchability attributes of the studied population to be expressed within a model selection framework, ideally characterized by the principles of parsimony and maximum likelihood, and (iii) the optimization of the use of information by embracing the opportunities that mark-recapture experiments generate to increase our knowledge of salmon ecology and hence improve both, future study designs and management decisions. Even if under particular circumstances the application of ad hoc approaches is considered to provide abundance estimates that are relatively unbiased and precise, only by following the two first recommendations above (at the very least) such confidence would be granted.

Lastly, much attention has been paid to the achievement of precision standards when estimating escapement in CTC Chinook indicator stocks (CV of 15%) but guidelines for enumeration experiments have not been specified yet. Given the deterministic nature of the CTC exploitation rate analysis, accuracy is of primary importance. Within the CWT system applied to Chinook salmon management, escapement is assumed to be unbiased for the purpose of expanding observed tagged fish to total tagged fish in the escapement (Pacific Salmon Commission Coded Wire Tag Workgroup 2008). Accuracy (or its lack of thereof) is directly connected to compliance with modelling assumptions; precision can be increased by overlooking model assumptions while compromising accuracy. The application of modern mark-recapture techniques in the present investigation responded mainly to concerns around the accuracy of estimates and the biological realism of models. In terms of precision, either the

Petersen or the best open-population models produced coefficients of variation lower than the CTC standard (5.7% and 9.5%, respectively) and lower than the 20% recommended in the mark-recapture literature (Pollock et al. 1990).

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7. TABLES

Table 1. Summary of encounter histories in the Atnarko 2009 mark-recapture experiment. Status after last encounter (SALE) is "at risk" when the individual was released alive after the last encounter and "not at risk" when the individual was found death or removed from the system at the last encounter.

Encounter history	SALE	Female	Male	Jack	Total	Cumulative
00001	Not at risk	1110	856	278	2244	2244
00010	Not at risk	333	263	36	632	2876
00100	At risk	8	66	36	110	2986
00100	Not at risk	227	133	9	369	3355
00101	Not at risk	1	8	3	12	3367
00110	At risk	0	16	2	18	3385
00110	Not at risk	0	1	0	1	3386
00111	Not at risk	0	1	0	1	3387
01000	At risk	83	187	36	306	3693
01000	Not at risk	79	41	3	123	3816
01001	At risk	1	0	0	1	3817
01001	Not at risk	40	32	6	78	3895
01010	At risk	4	16	0	20	3915
01010	Not at risk	5	1	0	6	3921
01011	Not at risk	3	3	0	6	3927
01100	At risk	4	16	2	22	3949
01101	Not at risk	1	3	0	4	3953
01110	At risk	2	5	1	8	3961
01110	Not at risk	0	1	0	1	3962
01111	Not at risk	0	1	0	1	3963
10000	At risk	58	96	28	182	4145
10001	Not at risk	26	16	3	45	4190
10010	At risk	8	13	2	23	4213
10010	Not at risk	5	3	0	8	4221
10011	Not at risk	1	2	0	3	4224
10100	At risk	3	10	0	13	4237
10101	Not at risk	4	3	0	7	4244
10110	At risk	1	1	0	2	4246
10110	Not at risk	1	0	0	1	4247
10111	Not at risk	1	1	0	2	4249
11000	At risk	5	7	3	15	4264
11010	At risk	0	1	0	1	4265
11010	Not at risk	3	1	0	4	4269
11100	At risk	0	1	1	2	4271
11110	Not at risk	0	2	0	2	4273

Table 2. Results of closure test for data scheme 902-15. See Appendix F for notation.

Stanley & Burnham Closure Test (Low p-values suggest population not closed):
Chi-square statistic=718.33630; df=43; p-value=0.00000

Otis et al. (1978) Closure Test (Low p-values suggest population not closed):
z-value= -3.74503; p-value= 0.00009

Component Statistics of Stanley & Burnham Closure Test

Component	Chi-square	df	p-value
Tests for additions to population (Low p-values suggest there were additions)			
NR vs JS	574.25259	12	0.00000
M_t vs NM	673.93006	23	0.00000
Tests for losses from population (Low p-values suggest there were losses)			
M_t vs NR	144.08371	31	0.00000
NM vs JS	44.40624	20	0.00133

Table 3. Results of closure test for data scheme 4273-5. See Appendix F for notation.

Stanley & Burnham Closure Test (Low p-values suggest population not closed):
Chi-square statistic= 261.92926; df=6; p-value= 0.00000

Otis et al. (1978) Closure Test (Low p-values suggest population not closed):
z-value=1.15349; p-value= 0.87564

Component Statistics of Stanley & Burnham Closure Test

Component	Chi-square	df	p-value
Tests for additions to population (Low p-values suggest there were additions)			
NR vs JS	72.47282	3	0.00000
M_t vs NM	154.68961	3	0.00000
Tests for losses from population (Low p-values suggest there were losses)			
M_t vs NR	189.45643	3	0.00000
NM vs JS	107.23965	3	0.00000

Table 4. Outcome of open-population model selection using the AIC framework. Models are defined by the probability of capture (p), the probability of survival (ϕ), and the probability of entering the system (b) under time-specific (t), group-specific (g), time- and group-specific (g*t), and/or invariant (*) conditions.

Model	AICc	AICc	Delta Weight	AICc Likelihood	# Parameters
{p(g), ϕ (*), b (g*t)}	2269.798	0.00	0.82930	1.0000	19
{p(g), ϕ (g), b (g*t)}	2273.955	4.16	0.10376	0.1251	21
{p(g), ϕ (t), b (g*t)}	2276.039	6.24	0.03660	0.0441	22
{p(*), ϕ (g), b (g*t)}	2276.429	6.63	0.03012	0.0363	19
{p(g), ϕ (g*t), b (g*t)}	2287.122	17.32	0.00014	0.0002	30
{p(*), ϕ (t), b (g*t)}	2288.309	18.51	0.00008	0.0001	20
{p(*), ϕ (g), b (t)}	2324.153	54.35	0.000	0.0000	11
{p(g), ϕ (*), b (t)}	2336.026	66.23	0.000	0.0000	11
{p(g), ϕ (t), b (t)}	2342.056	72.26	0.000	0.0000	14
{p(*), ϕ (t), b (t)}	2348.141	78.34	0.000	0.0000	12
{p(*), ϕ (*), b (g*t)}	2651.054	381.26	0.000	0.0000	17
{p(g), ϕ (t), b (*)}	3190.860	921.06	0.000	0.0000	11
{p(g), ϕ (g*t), b (t)}	5021.898	2752.1	0.000	0.0000	22
{p(g), ϕ (*), b (*)}	5380.264	3110.4	0.000	0.0000	8
{p(*), ϕ (t), b (g)}	53605.984	51336.0	0.000	0.0000	11
{p(g), ϕ (g), b (g)}	416630.46	414360	0.000	0.0000	12
{p(g), ϕ (*), b (g)}	416635.88	414366	0.000	0.0000	10
{p(*), ϕ (g), b (g)}	416645.25	414375	0.000	0.0000	10
{p(*), ϕ (*), b (*)}	416674.54	414404	0.000	0.0000	6

Table 5. Real function parameters of the best open-population model $\{p(g), \phi(*), b(g*t)\}$ from the mark-recapture experiment in 2009 Atnarko Chinook salmon escapement. Subscripts f, m, and j indicate female, male, and jack and subscripts 1, 2, 3, 4 indicate sampling interval. Spawning escapement estimates (N) are shown in the last three rows of the table.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1: ϕ	1.000	0.116E-005	0.999	1.000
2: p_f	0.151	0.012	0.129	0.176
3: p_m	0.123	0.008	0.108	0.140
4: p_j	0.069	0.0133	0.047	0.100
5: $b_{f,1}$	0.097	0.014	0.073	0.128
6: $b_{f,2}$	0.039	0.0160	0.017	0.086
7: $b_{f,3}$	0.106	0.018	0.075	0.147
8: $b_{f,4}$	0.663	0.016	0.629	0.695
9: $b_{m,1}$	0.150	0.017	0.119	0.187
10: $b_{m,2}$	0.467E-009	0.395E-010	0.390E-009	0.545E-009
11: $b_{m,3}$	0.046	0.019	0.020	0.103
12: $b_{m,4}$	0.642	0.019	0.603	0.679
13: $b_{j,1}$	0.046	0.024	0.016	0.127
14: $b_{j,2}$	0.159E-004	0.004	0.113E-221	1.000
15: $b_{j,3}$	0.103E-034	0.179E-035	0.684E-035	0.138E-034
16: $b_{j,4}$	0.825	0.017	0.789	0.857
17: N_f	8231.783	615.212	7138.119	9558.919
18: N_m	7876.714	513.213	6951.252	8968.637
19: N_j	4158.581	796.566	2895.793	6073.093

Table 6. Outcome of closed-population Otis et al. (1978) model selection using the AIC framework. Models are defined by the probability of capture (p) and the probability of recapture (c) under time-specific (t), group-specific (g), time- and group-specific (g*t), and/or invariant (*) conditions. Note: Model {p(t)=c(t)} corresponds to the M_t model used in the closure test.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	# Par	Deviance
{p(g*t)=c(g*t)}	-41213.207	0.00	1.00000	1.0000	18	2804.539
{p(t)=c(t)}	-41112.490	100.72	0.00000	0.0000	8	2925.284
{p(*),c(*)}	-38797.718	2415.4	0.00000	0.0000	5	5246.059
{p(g)=c(g)}	-38155.270	3057.9	0.00000	0.0000	6	5886.507
{p(*)=c(*)}	-38137.503	3075.7	0.00000	0.0000	4	5908.276

Table 7. Real function parameters of the best closed-population model $\{p(g^*t)=c(g^*t)\}$ from the mark-recapture experiment in 2009 Atnarko Chinook salmon escapement. Subscripts f, m, and j indicate female, male, and jack and subscripts 1, 2, 3, 4, 5 indicate sampling occasions. Spawning escapement estimates (N) are shown in the last three rows of the table.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1: $p_{f,1}$	0.0276041	0.0030532	0.0222103	0.0342620
2: $p_{f,2}$	0.0542564	0.0048525	0.0454945	0.0645916
3: $p_{f,3}$	0.0613590	0.0053877	0.0516105	0.0728076
4: $p_{f,4}$	0.0936793	0.0078168	0.0794411	0.1101642
5: $p_{f,5}$	0.3346224	0.0258227	0.2860450	0.3869780
6: $p_{m,1}$	0.0330897	0.0032175	0.0273319	0.0400105
7: $p_{m,2}$	0.0674520	0.0053066	0.0577660	0.0786266
8: $p_{m,3}$	0.0575590	0.0047526	0.0489214	0.0676132
9: $p_{m,4}$	0.0731203	0.0058051	0.0625264	0.0853456
10: $p_{m,5}$	0.2167056	0.0150444	0.1886688	0.2476370
11: $p_{j,1}$	0.0184154	0.0044417	0.0114575	0.0294727
12: $p_{j,2}$	0.0258811	0.0058090	0.0166324	0.0400631
13: $p_{j,3}$	0.0269167	0.0060043	0.0173437	0.0415502
14: $p_{j,4}$	0.0205289	0.0048543	0.0128896	0.0325465
15: $p_{j,5}$	0.1478695	0.0281150	0.1007663	0.2118049
16: N_f	4202.2703	260.77204	3747.9100	4775.7616
17: N_m	4714.4645	269.04124	4233.1210	5291.2675
18: N_j	2009.1883	357.41223	1450.5345	2879.4580

Table 8. Results of likelihood-ratio tests for closed-population models. Models are defined by the probability of capture (p) and the probability of recapture (c) under time-specific (t), group-specific (g), time- and group-specific (g*t), and/or invariant (*) conditions. (****) indicates the test is not applicable between no-nested models.

Reduced Model	General Model	Chi-sq.	df	Prob.
{p(t)=c(t)}	{p(g*t)=c(g*t)}	120.745	10	<.0001
{p(*),c(*)}	{p(g*t)=c(g*t)}	2441.521	13	<.0001
{p(g)=c(g)}	{p(g*t)=c(g*t)}	3081.968	12	<.0001
{p(*)=c(*)}	{p(g*t)=c(g*t)}	3103.737	14	<.0001
{p(*),c(*)}	{p(t)=c(t)}	2320.776	3	<.0001
{p(g)=c(g)}	{p(t)=c(t)}	2961.223	2	<.0001
{p(*)=c(*)}	{p(t)=c(t)}	2982.992	4	<.0001
{p(*),c(*)}	{p(g)=c(g)}	-640.447	1	****
{p(*)=c(*)}	{p(*),c(*)}	662.217	1	<.0001
{p(*)=c(*)}	{p(g)=c(g)}	21.769	2	<.0001

8. FIGURES

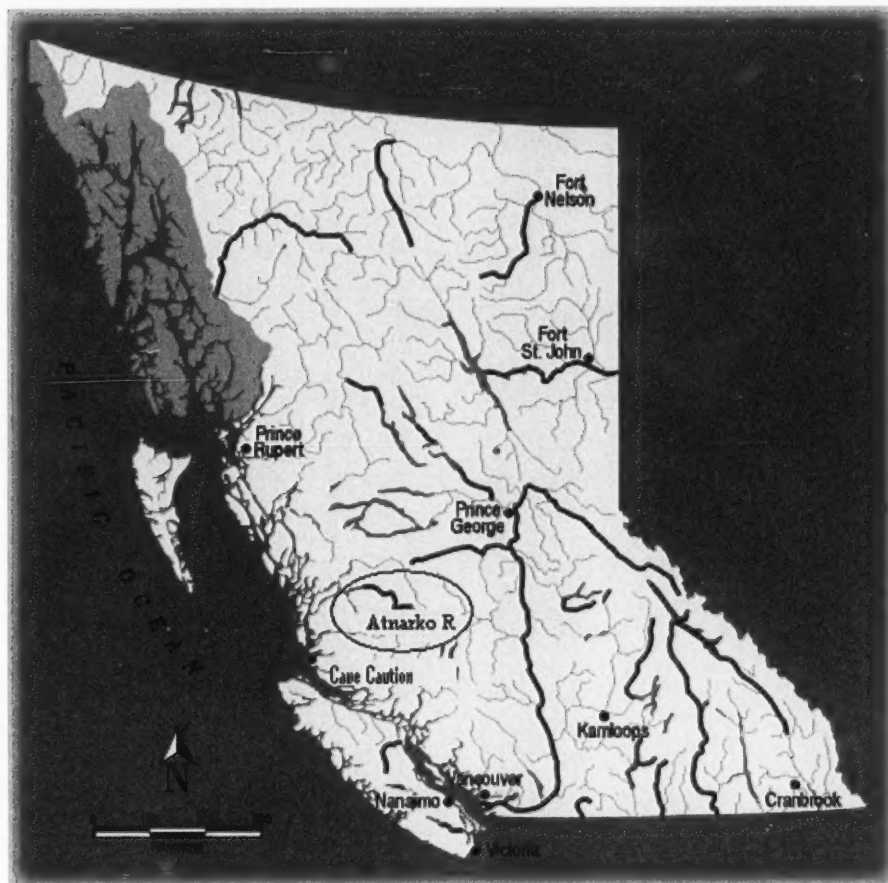


Figure 1. Map of British Columbia showing location of the Atnarko River.

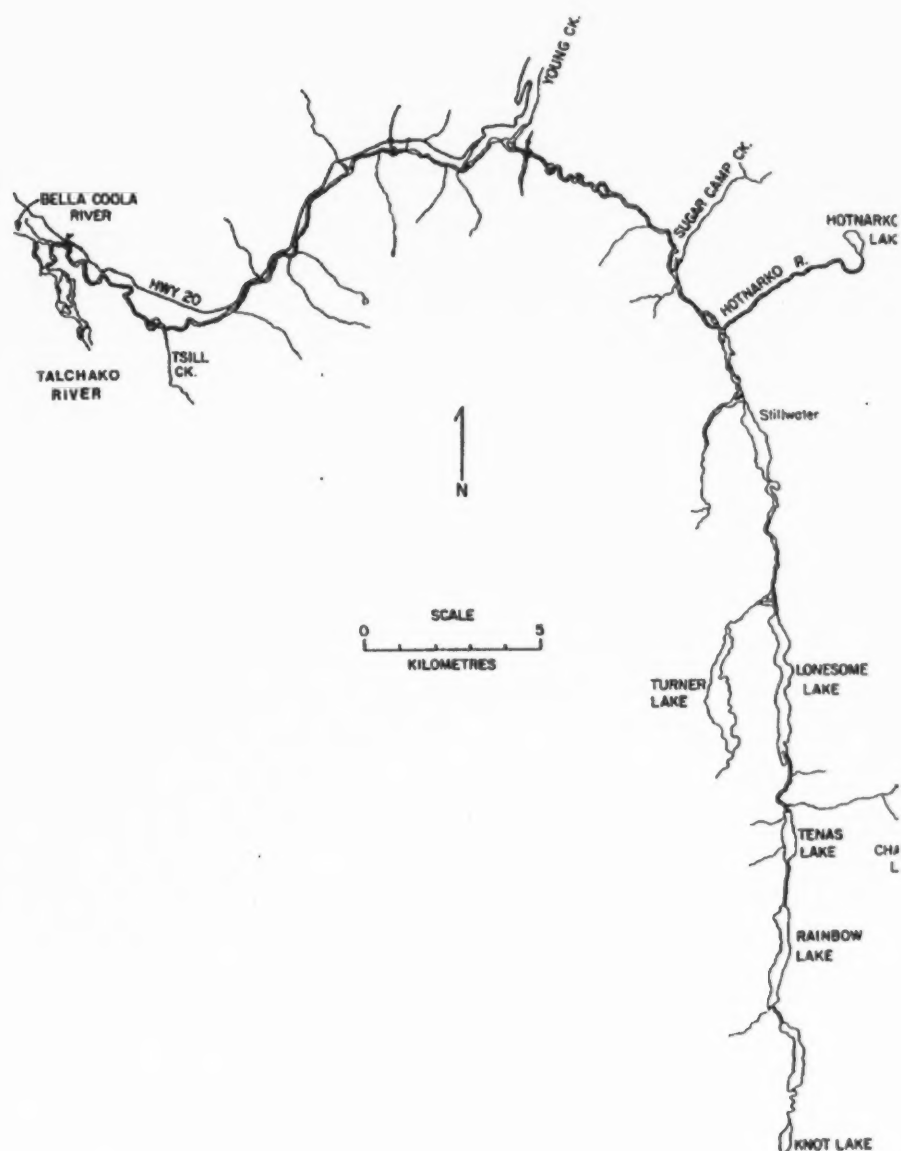


Figure 2. The Atnarko River drainage.

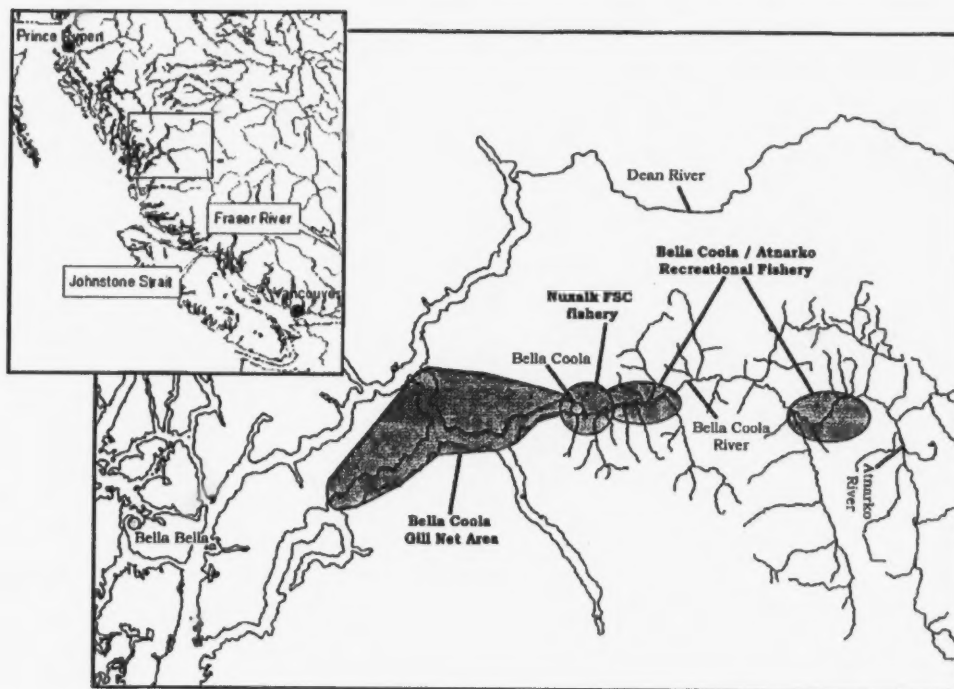


Figure 3. Coast of British Columbia and the Bella Coola fishing areas.
(Based on a map provided by Kay Kennes, Fisheries and Oceans Canada, Vancouver).

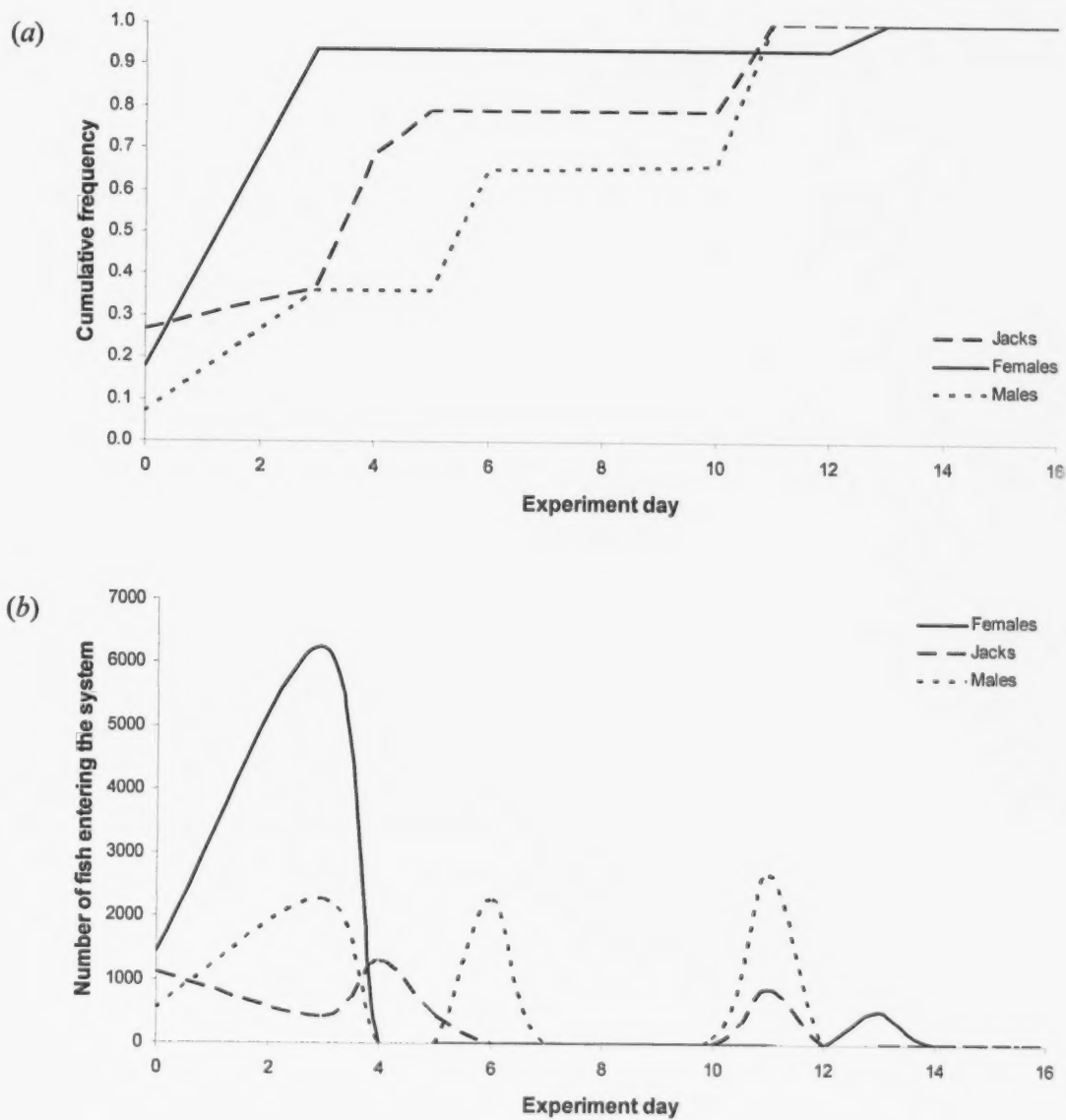


Figure 4. Spawning-run phenologies of females, males, and jacks in the 2009 Atnarko Chinook salmon escapement. Cumulative frequencies (a) and absolute abundance pulses (b) are shown.

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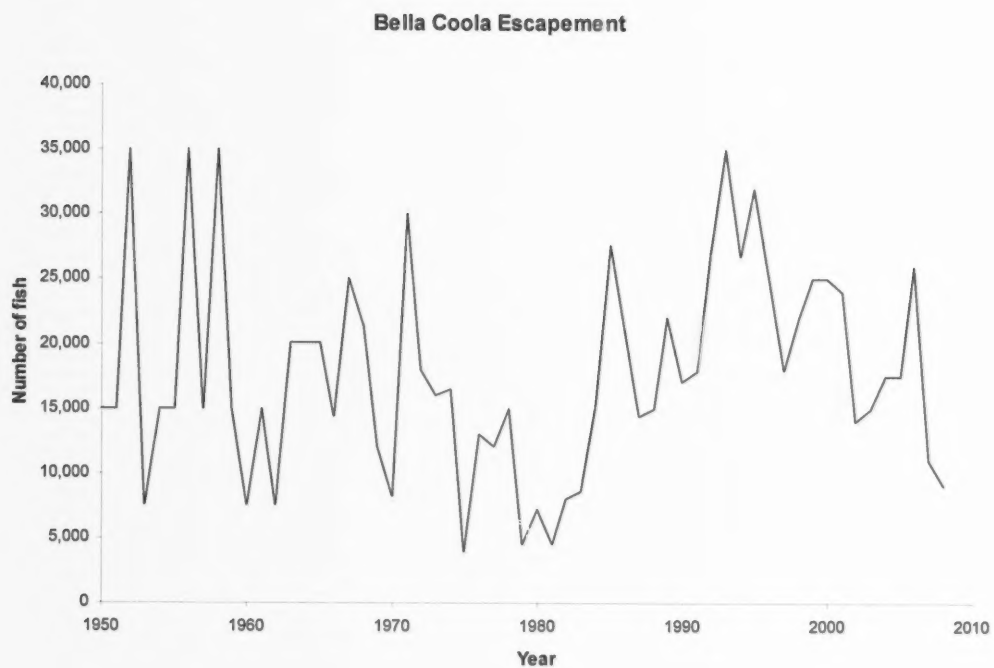
9. APPENDIXES

Appendix A. Percent distribution of Atnarko River Chinook CWT's estimated for PSC fisheries.

Catch Year	Alaska Net	Alaska Sport	Alaska Troll	Central Sport	Central Troll	Northern Sport	Northern Troll	NWVI Troll	Oregon Sport	SWVI Troll	WA Coast Sport	WA Troll
1989	0.4%	0.0%	0.0%	0.0%	0.0%	0.0%	99.6%	0.0%	0.0%	0.0%	0.0%	0.0%
1990	4.2%	0.0%	83.9%	0.0%	11.9%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
1991	0.0%	0.0%	61.0%	7.7%	3.7%	11.6%	11.1%	4.9%	0.0%	0.0%	0.0%	0.0%
1992	9.3%	0.0%	41.2%	5.7%	22.6%	10.9%	8.3%	0.0%	0.7%	1.3%	0.0%	0.0%
1993	2.8%	2.4%	52.6%	6.8%	5.1%	9.2%	19.3%	1.8%	0.0%	0.0%	0.0%	0.0%
1994	2.8%	2.3%	31.5%	5.9%	24.3%	19.1%	14.1%	0.0%	0.0%	0.0%	0.0%	0.0%
1995	3.4%	12.6%	46.5%	7.2%	3.2%	15.6%	11.4%	0.0%	0.0%	0.0%	0.0%	0.0%
1996	0.0%	9.8%	52.1%	21.4%	0.0%	16.7%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
1997	3.0%	18.9%	39.4%	8.0%	2.9%	23.1%	4.6%	0.0%	0.0%	0.0%	0.0%	0.0%
1998	0.0%	3.2%	75.0%	9.0%	0.0%	12.8%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
1999	17.3%	17.2%	37.2%	7.7%	0.0%	19.3%	0.0%	0.0%	0.0%	0.0%	0.0%	1.4%
2000	0.7%	0.0%	86.8%	0.0%	0.0%	7.5%	0.0%	0.0%	0.0%	5.0%	0.0%	0.0%
2001	0.0%	17.5%	55.1%	10.5%	0.0%	14.4%	0.0%	0.0%	0.0%	0.0%	2.6%	0.0%
2002	2.1%	2.8%	23.0%	7.5%	0.0%	26.4%	33.8%	4.4%	0.0%	0.0%	0.0%	0.0%
2003	0.4%	0.0%	22.0%	44.2%	0.0%	20.5%	12.8%	0.0%	0.0%	0.0%	0.0%	0.0%
2004	0.0%	0.0%	45.7%	25.4%	0.0%	12.4%	16.6%	0.0%	0.0%	0.0%	0.0%	0.0%
2005	0.5%	2.5%	37.1%	22.0%	0.0%	25.6%	12.4%	0.0%	0.0%	0.0%	0.0%	0.0%
2006	0.0%	5.6%	38.5%	21.8%	0.0%	22.4%	11.7%	0.0%	0.0%	0.0%	0.0%	0.0%
2007	0.0%	11.7%	54.7%	0.0%	0.0%	27.1%	3.5%	3.0%	0.0%	0.0%	0.0%	0.0%
(89-98)	2.6%	4.9%	48.3%	7.2%	7.4%	11.9%	16.8%	0.7%	0.1%	0.1%	0.0%	0.0%
(99-07)	2.3%	6.3%	44.5%	15.4%	0.0%	19.5%	10.1%	0.8%	0.0%	0.6%	0.3%	0.2%

Appendix B. Methods used to estimate escapement of Chinook salmon in the Bella Coola watershed. Shaded rows indicate years were mark-recapture programs constituted an estimation method.

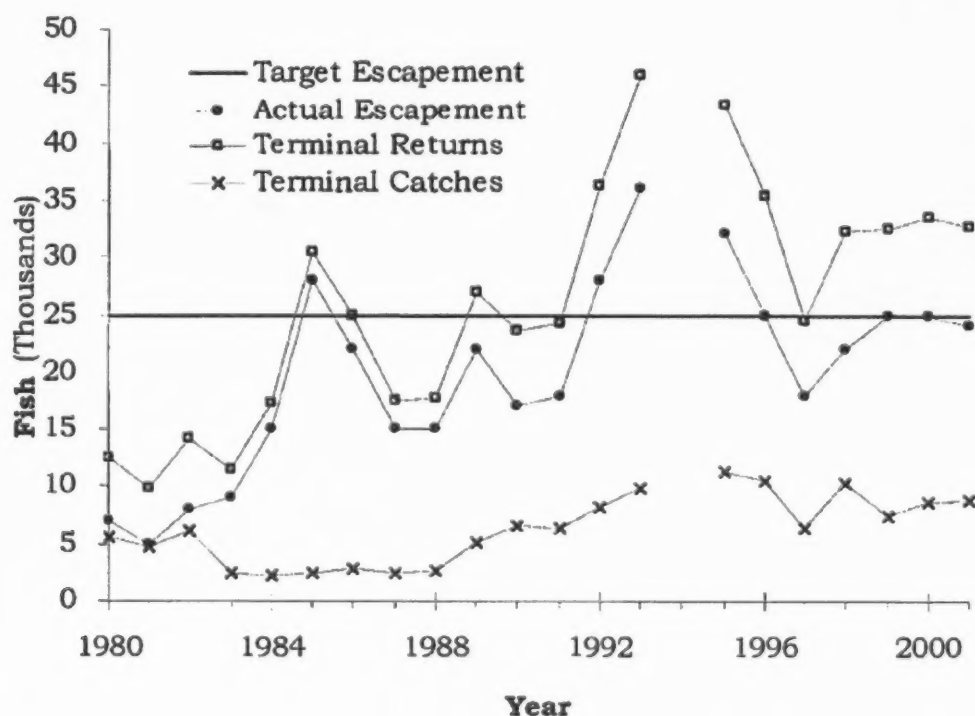
Year	Escapement	Methods
2008	9,000	Float Count
2007	11,000	Average of peak drift count, brood stock capture CPUE and number of carcasses pitched
2006	26,000	Average of peak drift count, brood stock capture CPUE and number of carcasses pitched
2005	17,500	Average of peak drift count, brood stock capture CPUE and number of carcasses pitched
2004	17,500	Average of peak drift count, brood stock capture CPUE and number of carcasses pitched
2003	15,000	Mark-recapture Petersen, peak drift count, brood stock capture CPUE and num of carcasses pitched
2002	14,000	Mark-recapture Petersen, peak drift count, brood stock capture CPUE and num of carcasses pitched
2001	24,000	Mark-recapture Petersen, peak drift count, brood stock capture CPUE and num of carcasses pitched
2000	25,000	Unknown, most likely aiks, drifts, visual counts
1999	25,000	Walk
1998	22,000	Based on floats, dead pitch data, chinook capture for enhancement
1997	18,000	Walk
1996	25,000	Float
1995	32,000	Unknown, most likely aiks, drifts, visual counts
1994	26,800	Walk, Float
1993	35,000	Walk, Float
1992	27,000	Walk, Float
1991	17,800	Walk, Float, Other
1990	17,000	Walk, Float, Heli
1989	22,000	Walk, Float, Other
1988	15,000	Walk, Float, Other
1987	14,425	Walk, Float
1986	21,300	Walk, Float, Heli, Dead Pitch, Tag Recovery, live spaghetti tagging and Carcass Tagging-numbered
1985	27,560	Carcass Tagging-color coded
1984	15,320	Carcass Tagging-not numbered, Stream Bank, Boat, Stream Walk
1983	8,600	Walks, drifts, visual counts
1982	8,000	Walks, drifts, visual counts
1981	4,500	Walks, drifts, visual counts
1980	7,200	Walks, drifts, visual counts
1979	4,500	Walks, drifts, visual counts
1978	15,000	Walks, drifts, visual counts
1977	12,000	Walks, drifts, visual counts
1976	13,000	Walks, drifts, visual counts
1975	4,000	Walks, drifts, visual counts
1974	16,500	Walks, drifts, visual counts
1973	16,000	Walks, drifts, visual counts
1972	18,000	Walks, drifts, visual counts
1971	30,000	Walks, drifts, visual counts
1970	8,250	Walks, drifts, visual counts
1969	12,000	Walks, drifts, visual counts
1968	21,300	Walks, drifts, visual counts
1967	25,000	Walks, drifts, visual counts
1966	14,400	Walks, drifts, visual counts
1965	20,000	Walks, drifts, visual counts
1964	20,000	Walks, drifts, visual counts
1963	20,000	Walks, drifts, visual counts
1962	7,500	Walks, drifts, visual counts
1961	15,000	Walks, drifts, visual counts
1960	7,500	Walks, drifts, visual counts
1959	15,000	Walks, drifts, visual counts
1958	35,000	Walks, drifts, visual counts
1957	15,000	Walks, drifts, visual counts
1956	35,000	Walks, drifts, visual counts
1955	15,000	Walks, drifts, visual counts
1954	15,000	Walks, drifts, visual counts
1953	7,500	Walks, drifts, visual counts
1952	35,000	Walks, drifts, visual counts
1951	15,000	Walks, drifts, visual counts
1950	15,000	Walks, drifts, visual counts



Appendix-B Figure. Time series of Chinook salmon escapement in the Bella Coola watershed. Values correspond to those shown in the previous table.

Appendix C. Observed escapement and catch of Atnarko Chinook 1980-2001.

Consistent post-season estimates of the total number of spawners (actual escapement), and catches from all three harvester groups (terminal catches) are available since 1980. Actual escapements, rounded to the nearest thousand, can be compared to the management goal of 25,000 spawners (target escapement). Terminal catches include all observed catches from the commercial fishery in the Bella Coola Gillnet Area, the Bella Coola / Atnarko recreational fishery, and the Nuxalk food fishery. Terminal returns are the sum of observed escapement and terminal catches. 1994 data are excluded due to problems with data collection. Figure used with permission from Pestal (2004).



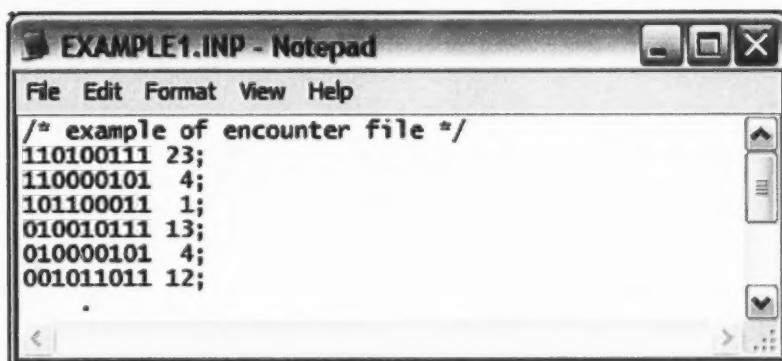
Appendix D. Atnarko Chinook Mark-Recapture Results, 2001-2003.

Year	Sex	No. Tags Applied	No. Tags Recovered	Total No. Carcasses Examined	Modified Peterson	95% lower limit	95% upper limit	Total Peterson Estimate	95% lower limit	95% upper limit	CV
2001	M	751	154	2054	9970	8523	11661	20769	17400	25125	5.6%
	F	562	131	2361	10074	8500	11937				
	J	39	7	144	725	377	1526				
	Total	1352	292	4559	20769	17400	25125				
Year	Sex	No. Tags Applied	No. Tags Recovered	Total No. Carcasses Examined	Modified Peterson	95% lower limit	95% upper limit	Total Peterson Estimate	95% lower limit	95% upper limit	CV
2002	M	268	36	839	6107	4448	8657	16352	11212	25168	11.7%
	F	229	33	1262	8544	6141	12257				
	J	43	2	115	1701	622	4253				
	Total	540	71	2216	16352	11212	25168				
Year	Sex	No. Tags Applied	No. Tags Recovered	Total No. Carcasses Examined	Modified Peterson	95% lower limit	95% upper limit	Total Peterson Estimate	95% lower limit	95% upper limit	CV
2003	M	470	63	837	6167	4837	7863	13433	10142	18625	8.5%
	F	399	82	1215	5860	4732	7249				
	J	76	3	72	1405	574	3513				
	Total	945	148	2124	13433	10142	18625				
										Average CV	8.6%

Appendix E. Data formatting and encounter histories for mark-recapture analyses ^a

The preferred format is the *encounter history*. The encounter history is a contiguous series of specific dummy variables, each of which indicates something concerning the encounter of that individual - for example, whether or not it was encountered on a particular occasion, how it was encountered, where it was encountered, and so forth. The particular encounter history will reflect the underlying model type you are working with (e.g., recaptures of live individuals, recoveries of dead individuals). Consider for example, the encounter history for a typical mark-recapture analysis (the encounter history for a mark-recapture analysis is often referred to as a *capture history*, since it implies physical capture of the individual). In most cases, the encounter history consists of a contiguous series of "1"s and "0"s, where "1" indicates that an animal was recaptured (or otherwise known to be alive and in the sampling area), and "0" indicates the animal was not recaptured (or otherwise seen). Suppose that August 15th is the first day of the study, and that August 27th is the last day of the study under a daily sampling schedule. If an individual was captured and marked during the first day of the study, was seen periodically until August 24th, when it was seen for the last time. The corresponding encounter-history for this individual would be: 1011000001000. In other words, the individual was seen in August 15th (the starting "1"), not seen in August 16th ("0"), seen in August 17th and 18th ("11"), not seen for the next 5 days ("00000"), seen again in August 24th ("1"), and then not seen again ("000").

Superficially, the encounter histories file is structurally quite simple. It consists of an ASCII (text) file, consisting of the encounter history itself (the contiguous string of dummy variables), followed by one or more additional columns of information pertaining to that history. Each record (i.e., each line) in the encounter histories file ends with a semi-colon. Consider the next table:



```
EXAMPLE1.INP - Notepad
File Edit Format View Help
/* example of encounter file */
110100111 23;
110000101 4;
101100011 1;
010010111 13;
010000101 4;
001011011 12;
```

Enclosed with /* and */ you can place any comment or additional information. In the above table each encounter history is followed by a number. This number is the frequency of all individuals having a particular encounter history. This is not required (and in fact isn't what you want to do if you're going to consider individual covariates - more on that later), but is often more convenient for large data sets. For example, the summary encounter history 110000101 4; could also be as:

```
110000101 1;
110000101 1;
110000101 1;
110000101 1;
```

Note again that each line - each 'encounter history record' ends in a semi-colon. How would you handle multiple groups? For example, suppose you were interested in males and females? In fact, it is relatively straightforward to format the data for multiple groups - very easy for summary encounter histories, a bit less so for individual encounter histories. In the case of summary encounter histories, you simply add a second column of frequencies to the encounter histories to correspond to the other sex. For example,

```
110100111 23 17;
110000101 4 2;
101100011 1 3;
```

In other words, 23 of one sex and 17 of the other have history "110100111" (the ordering of the sexes - which column of frequencies corresponds to which sex - is entirely up to you). If you are using individual records, rather than summary frequencies, you need to indicate group association in a slightly less-obvious way - you will have to use a '0' or '1' within a group column to indicate the frequency - but obviously for one group only. Let's demonstrate the idea here. Suppose we had the following summary history, with frequencies for males and females (respectively):

```
110000101 4 2;
```

In other words, 4 males, and 2 females with this encounter history (note: the fact that males come before females in this example is completely arbitrary. You can put whichever sex - or 'group' - you want in any column you want - all you'll need to do is remember which columns in the file correspond to which groups). To 'code' individual encounter histories, the text file would be modified to look like:

```
110000101 1 0;
110000101 1 0;
110000101 1 0;
110000101 1 0;
110000101 0 1;
110000101 0 1;
```

In this example, the coding '1 0' indicates that the individual is a male (frequency of 1 in the male column, frequency of 0 in the female column), and '0 1' indicates the individual is a female (frequency of 0 in the male column, and frequency of 1 in the female column). The use of one-record per individual is only necessary if you're planning on using individual covariates in your analysis. Therefore, for the kind of analyses we are planning to conduct, it would be preferable the frequencies format.

In the preceding example, we had 2 groups: males and females. The frequency of encounters for each sex is coded by adding the frequency for each sex to the right of the encounter history. But, what if you had something like males, and females (i.e., data from both sexes) and good colony and poor colony (i.e., data were sampled for both sexes from each of 2 different colonies - one classified as good, and the other as poor). How do you handle this in the text file? Well, all you need to do is have a frequency column for each (sex, colony) combination: one frequency column for females from the good colony, one frequency column for females from the poor colony, one frequency column for males from the good colony, and finally, one frequency column for males from the poor colony. An example of such a file is shown below:

```
multi_group.inp - Notepad
File Edit Format View Help
/= females, good - females, poor - males, good - males, poor */
00010 150 145 171 167;
00011 200 205 179 183;
00100 213 198 131 77;
00101 14 26 32 50;
00110 54 59 95 101;
00111 69 67 92 122;
01000 93 64 74 51;
```

This is a format that we could use to stratify by sex and reach or river segment.

Occasionally, you may choose to remove individuals from the data set at a particular occasion. For example, because your experiment requires you to remove the individual after its first recapture, or because it is injured, or for some other reason. The standard encounter history we have looked at so far records presence or absence only. How do we accommodate "removals (e.g., mortalities)" in the text file? Actually, its very easy - all you do is change the "sign" on the frequencies from positive to negative. Negative frequencies indicates that that many individuals with a given encounter history were removed from the study. For example,

```
100100 1500 1678;  
100100 -23   -25;
```

In this example, we have 2 groups, and 6 occasions. In the first record, we see that there were 1500 individuals and 1678 individuals in each group marked on the first occasion, not encountered on the next 2 occasions, seen on the fourth occasion, and not seen again. In the second line, we see the same encounter history, but with the frequencies "-23" and "-25". The negative values indicates that 23 and 25 individuals in both groups were marked on the first occasion, not seen on the next 2 occasions, were encountered on the fourth occasion, at which time they were removed from the study. Clearly, if they were removed, they cannot have been seen again.

Finally, the time intervals between sampling occasions do not necessarily have to be the same, but this is an attribute that is not included in the encounter history per se but in the text file as a comment using /* */. For example,

```
/* Estimating salmon numbers returning to spawn in Chase River 1989 */  
/* These are the male salmon with two groups. */  
/* Group1 = adults . group2=jacks */  
/* Survey conducted over 10 weeks. Weeks 1 & 2 pooled. weeks 9 & 10 pooled */
```

The time intervals between sampling events is used latter on during the parameterization of the model.

a Partly extracted from: Cooch, E., and White G. (Eds). Program MARK: a gentle introduction. 8th Edition.
 <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>.

Appendix F. Glossary of terms used in the outcome of the closure test.

Chi-square statistic - This is equivalent to in Stanley and Burnham (1999), and is the test statistic for the overall closure test presented in that paper. Extreme values of this statistic result in low p -values, and suggests the population is not closed.

M_t - This is equivalent to M_t in Otis et al. (1978), and represents the closed-population capture-recapture model allowing for time variation in capture probabilities.

M_t vs NM - This component test evaluates whether there is evidence of additions to the population. It tests the fit of the closed-population model M_t ($H_0: M_t$) against the No-mortality model ($H_a: NM$) as a specific alternative.

M_t vs NR - This component test evaluates whether there is evidence of losses from the population. It tests the fit of the closed-population model M_t ($H_0: M_t$) against the No-recruitment model ($H_a: NR$) as a specific alternative.

NM vs JS - This component test evaluates whether there is evidence of losses from the population. It tests the fit of the No-mortality model ($H_0: NM$) against the Jolly-Seber model ($H_a: JS$) as a specific alternative.

NR vs JS - This component test evaluates whether there is evidence of additions to the population. It tests the fit of the No-recruitment model ($H_0: NR$) against the Jolly-Seber model ($H_a: JS$) as a specific alternative.

z-value - The computed value of the closure test statistic described in Otis, et al. (1978). Extreme values of this statistic result in low p -values, and suggests the population is not closed.



